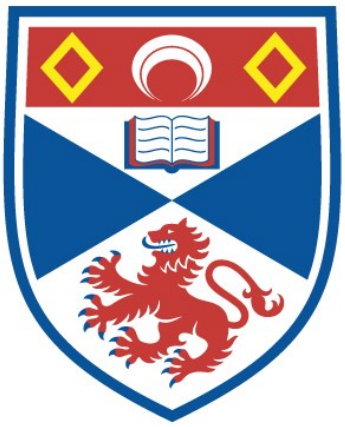
TEMPORAL CONTEXT, OBJECT PERMANENCE, AND SPACE

Christopher I. Baker

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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A thesis submitted to the University of St Andrews for the degree of Doctor of Philosophy

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ABSTRACT

In everyday life objects are continually moving into and out of view, yet we experience a stable environment in which objects are "permanent" and have an existence independent of observation. Many non-human species also exhibit such "object permanence", although the nature of their representations of occluded objects remains unclear. This thesis investigated knowledge and representation of occluded objects in Rhesus macaques (*Macaca mulatta*). At the behavioural level, an analysis of the reaching behaviour of a macaque demonstrated representation for the motivational value of rewards hidden from sight, and provided some evidence for the representation of object form. At the neural level, a population of cells was found in the superior temporal sulcus of macaques that might contribute to object permanence. The cells showed prolonged responses as objects moved gradually out of sight behind occluding screens. This activity was selective for the location of occlusion and did not develop fully until complete occlusion of the object. A small population of bimodal (auditory-visual) cells showed related activity with modulation of response to an auditory stimulus dependent on whether the sound source was in or out of sight. An influence of the position of the stimuli was also observed for these cells. An analysis of cells with diverse response characteristic revealed that positional sensitivity was not limited to a small sub-group of cells within the superior temporal sulcus. This is the first evidence for spatial coding in temporal cortex, a region associated with object recognition.

Keywords: object permanence, macaque, STS, multisensory integration, occlusion, spatial coding, dorsal and ventral streams

CHAPTER 1

GENERAL INTRODUCTION

1.1 Background to study

The experiments described in this thesis are: (a) a behavioural study of the extent of macaque knowledge about occluded objects; (b) neurophysiological studies of visual occlusion, auditory-visual interactions and positional sensitivity in the superior temporal sulcus of the macaque.

The superior temporal sulcus (STS) is a brain region associated with the high level processing of visual information and contains neurones that respond to the sight of biologically significant stimuli such as faces, bodies, hand actions, and "biological motion" such as walking (e.g. Perrett *et al.*, 1982, 1985, 1989, 1992). Given these responses, the superior temporal sulcus has been argued to play a critical role in the visual recognition of objects and, more specifically, in social cognition.

The driving force behind the studies presented here was the question of how the brain produces a stable representation of objects in the environment. Objects are continually moving into and out of view and our perception of them is discontinuous. We have the impression that objects exhibit "permanence" and exist independently of our perception of them, but how does such an impression arise? How do we distinguish an object that has ceased to exist from one that has maintained existence but is not visible? The direct perceptual evidence available is the same. Early studies of infants' search behaviour suggested that their perception

of the world is very different from that of an adult - "out of sight" may not be just "out of mind" but "out of existence". Phenomenological studies in adults have suggested that the visual cues associated with an object being destroyed and an object moving temporarily out of sight are sufficient to distinguish continued existence from annihilation.

Studies of search behaviour in non-humans have shown a similar pattern of development to human infants, although many species fail to exhibit the same behaviour as fully developed humans. Monkeys (e.g. macaques) will search for hidden objects, but the nature of their representations about the hidden objects is unclear.

Although there have been many behavioural studies of occlusion, little is known about the neurophysiological mechanisms involved in maintaining a continuous representation of objects despite discontinuous perception.

1.2 Techniques for studying brain function

Many different techniques are available for studying the neural processing of visual information within the brain. Different techniques carry different costs and benefits and the suitability of a particular technique depends on the nature of the questions being asked. In this section I will briefly review some of the available techniques and discuss the advantages and limitations of single cell recording. Studies using many of these different techniques will be reviewed throughout this thesis.

Dysfunction of a brain region can provide information about the role of the damaged structures. In humans, such dysfunction may arise as a result of head injury

or a stroke. The lesions present in such neuropsychological subjects may be large involving damage to many different structures, making the attribution of function to different areas difficult. Evidence for dissociation of function between different areas, however, may become apparent by contrasting patients with lesions to different brain systems.

In laboratory animals, the site and extent of brain lesions can be controlled and the role of specific brain areas targeted. Impairment in a given behaviour following removal of a particular structure, however, tells little about the nature of involvement of that structure in normal behaviour. Implication of function is often a complicated deduction.

In recent years, the use of non-invasive functional imaging techniques (e.g. positron emission tomography or PET and functional magnetic resonance imaging or fMRI) has increased dramatically. Such techniques can be applied to humans performing simple tasks. PET measures relative blood flow changes in the brain following administration of positron-emitting radioisotopes (e.g. oxygen-15 in water - $H_2{}^{15}O$) into the body systemically. In contrast, fMRI measures changes in the vascular concentration of deoxyhaemoglobin, which is paramagnetic. Such measures are assumed to reflect the level of neural activity in a given brain region. The principal method of analysis behind the use of these techniques involves "cognitive subtraction". The activity in the brain is recorded during the performance of two tasks, the difference between the two tasks representing the function of interest. For example task A may involve the cognitive functions x and y, whereas task B may only engage function x. Subtracting the activity observed in task B from that in task A highlights the areas of activity associated with function y only.

The temporal resolution of such imaging techniques is at best in the order of seconds and more frequently assessments are made over much longer time periods (up to a minute for PET). The spatial resolution is in the order of millimetres and therefore not high enough to visualise cortical columns. These techniques can help provide answers to the question of where in the brain particular functions are operating, creating functional anatomical maps (although, see Friston, 1998 for discussion of recent developments).

None of the techniques discussed so far provide any direct information on the mechanisms of brain function. They may implicate a given region in a particular function, but do not indicate the nature of involvement. Moreover, lack of differential brain activity in functional imaging measures of control and experimental tasks cannot be taken to imply lack of differential cellular activity. For example, 2 cell populations each activated selectively by experimental and control tasks may co-exist in the same area.

Using an array of electrodes on the surface of the scalp event related potentials or ERPs can be recorded. Although the temporal resolution of this technique (in the order of milliseconds) is much higher than either PET or fMRI, the spatial resolution is poor. The technique can, however, provide evidence for the operation of different mechanisms in separate brain functions.

In comparison with the previous techniques discussed, single cell recording provides much better spatial resolution, operating at the level of the single cell. The temporal resolution is equivalent to that from the recording of ERPs. Single cell recording can provide information about the neural processing mechanisms operating in the brain, addressing the nature of involvement of a given brain area. It can provide direct insight into the computational steps involved in a given process

and is the principal method followed in this thesis. Deduction of function from cellular activity alone, however, may require complicated inferences.

Ultimately, converging evidence from many techniques will provide the best insight into the neural processing of visual information.

1.3 The rhesus macaque (*Macaca mulatta*)

The rhesus macaque is an Old World monkey and a close relative of humans in phylogenetic terms. Chimpanzees represent the closest living relative to humans, but are considered to be too close for experimentation to be ethical. Macaques are highly visual animals with over half the surface area of the neocortex involved in the processing of visual information (Felleman and Van Essen, 1991). They live in large groups and demonstrate complex social behaviour with defined hierarchies. Visual signals (e.g. representing threat or submission) form an important part of social behaviour.

The visual system of the rhesus macaque has been extensively studied and much is known about the anatomy, connections and neurophysiology of the visual system. Given this background, the macaque is an excellent subject for elucidating complex visual function.

1.4 Thesis overview

The background for the experiments described in this thesis is presented in chapters 2 and 3, covering the anatomy and neurophysiology of the superior temporal sulcus and object permanence, respectively. The review of the superior

temporal sulcus is presented in the light of the proposed division of cortical visual processing into separate dorsal and ventral streams. Different frames of reference for processing visual information about objects are discussed.

The superior temporal sulcus contains heterogeneous populations of cells along its length with a polysensory region located in the upper bank. The visual modality appears to be dominant and has been the focus of much of the research in this brain area. Very little is known about the functional organisation of the cells, and the prediction from anatomy of convergence of spatial and object processing has not been confirmed neurophysiologically.

Object permanence, and all that the concept entails, has been much studied in the context of child development. There have also been a number of comparative psychological studies, but many of these suffer from too stringent an adherence to the methodology used in testing human infants, failing to take account of species differences.

In chapter 4, I will present an experiment that was largely a replication of work by Tinklepaugh (1928) on the nature of macaque representations of occluded objects. The experiment was aimed at determining whether there is any evidence for the representation of the form of hidden objects as well as confirming Tinklepaugh's (1928) finding for representation of motivational value.

The remaining chapters of the thesis describe a series of neurophysiological studies, and the general experimental methods for these studies are outlined in chapter 5.

The experiment described in chapter 6 was designed to investigate the responses of cells in the anterior superior sulcus during the temporary occlusion (3-

20 seconds) of visual stimuli. Responses were found during the period of occlusion and these may relate to object permanence.

A small number of cells with bimodal (auditory-visual) properties were discovered with responses also related to the occlusion of visual stimuli. During testing the source of sound was either in- or out-of-sight. The responses of these cells, reported in chapter 7, showed modulation of activity elicited by an auditory stimulus depending on the concurrent visual stimulus.

A significant finding in the cells described in chapters 6 and 7 was sensitivity to the position of stimuli within the room. Coding of position has generally been considered the domain of the dorsal stream of cortical processing. In chapter 8, a review of evidence for the coding of position in ventral brain areas is presented, along with further data from cells in the superior temporal sulcus suggesting the presence of positional sensitivity.

The final chapter of the thesis presents a summary of the findings and a discussion of their significance with particular emphasis on social cognition.

CHAPTER 2

VISUAL PROCESSING IN THE TEMPORAL CORTEX

2.1 INTRODUCTION

For primates, vision is a critical sense and the processing of visual information occupies large regions of the cortex. Within the macaque visual system Felleman and Van Essen (1991) identified 32 different cortical areas subserving visual functions constituting 55% of the surface area of the neocortex. Visual specialisation may underlie the evolution of the large brains of primates and may be associated with the development of frugivory (Barton, 1998) or complex social behaviour (Barton, 1996).

The anatomy and connections of visual processing in the brain have been extensively reviewed elsewhere and will not be covered in detail here (e.g. Maunsell and Newsome, 1987; DeYoe and Van Essen, 1988; Felleman and van Essen, 1991; Bullier and Nowak, 1995). In this chapter I will focus on the proposed segregation of visual processing into two cortical streams (e.g. Ungerleider and Mishkin, 1982) and the position of the anterior superior temporal sulcus within the visual system hierarchy and its relation to these two streams.

2.2 TWO CORTICAL STREAMS

Primarily on the basis of lesion studies of primates, Ungerleider and Mishkin (1982; see also Mishkin *et al.*, 1983) proposed the separation of visual processing

into two separate cortical "streams". Monkeys with lesions of the posterior parietal cortex were found to be impaired on a spatial task, the "landmark" task, in which the monkey is rewarded for choosing a food well nearest to an object or "landmark". These monkeys were relatively unimpaired, however, on a task requiring object discrimination. Conversely, monkeys with lesions of the inferotemporal cortex were impaired on the object discrimination task but relatively unimpaired on the landmark task. Such a division of the visual system has been supported by further anatomical studies in non-human primates (e.g. Baizer *et al.*, 1991; Morel and Bullier, 1990) and by neuropsychological (e.g. Newcombe *et al.*, 1987) and functional imaging studies in humans (e.g. Haxby *et al.*, 1991, 1993; Köhler *et al.*, 1995). Topological analysis (Young, 1992; Young *et al.*, 1995; Jouve *et al.*, 1998) of the primate visual system (based on the presence and number of different connections between areas) also suggests a division into separate dorsal and ventral streams with limited interaction between the streams.

The division of function between dorsal and ventral streams has often been termed "what" versus "where", but an alternative view, advanced by Milner and Goodale (Goodale and Milner, 1992; Milner and Goodale, 1993, 1995), suggests that "what" versus "how" is a more appropriate dichotomy. Focusing on the outputs of the system rather than the inputs, they have emphasised the visuomotor nature of processing within parietal areas (e.g. see Rizzolatti *et al.*, 1994 for brief review). The two visual pathways may then be seen as subserving object/scene recognition and visuomotor behaviour, respectively. One implication of this model is that form and space may be processed in both pathways but for different functions. For example, information about form is required for both identifying and picking up an object, but

Milner and Goodale suggest the involvement of different cortical pathways in processing the form information for the two tasks.

In support of their argument, Milner and colleagues (e.g. Goodale *et al.*, 1991; Milner *et al.*, 1991; Milner, 1997) have reported a visual form agnosic, DF, with impaired ability to perform perceptual discriminations of visual features, but intact ability to perform actions dependent on the same featural characteristics. For example, DF is completely unable to indicate the orientation of a slot in a disc, but if asked to put her hand through the slot performs "unhesitatingly and accurately" (Milner *et al.*, 1991; Goodale *et al.*, 1991). Thus, information about the orientation of the slot is available for action, but not for perception. Similarly, she cannot indicate the width of a rectangular block with her index finger and thumb, but shows intact ability to reach out and pick up the block in a manner similar to normal subjects. For example, during the reaches, the aperture between her index finger and thumb showed anticipation of the width of the block (Milner *et al.*, 1991; Goodale *et al.*, 1991).

Structural MRI has shown that DF has damage in prestriate areas 18 and 19 (Milner *et al.*, 1991) and this has been assumed to represent damage within the ventral stream of cortical visual processing (Milner, 1997).

Neurophysiological evidence supports a visuomotor/object recognition distinction for the two streams of cortical visual processing. In inferior temporal cortex, cells are found that respond selectively to complex visual stimuli. These cells show stimulus invariance in that they maintain this selectivity over changes in stimulus size (e.g. Ito *et al.*, 1995), partial occlusion (Kovács *et al.*, 1995), defining cue (e.g. luminance, texture or relative motion – Sáry *et al.*, 1993) and position (e.g. Lueschow *et al.*, 1994; Ito *et al.*, 1995). These properties suggest coding for abstract

stimulus shapes (i.e. coding for shape independent of the conditions under which shapes are observed) and are entirely consistent with a role in object recognition. Such cellular characteristics correspond with our ability to recognise objects despite profound changes in the retinal image (e.g. Vogels and Orban, 1996).

In contrast, cells in parietal cortex show responses related to reaching and grasping (e.g. Mountcastle *et al.*, 1975; Taira *et al.*, 1990; see Jeannerod *et al.*, 1995 for recent review), motion perception and eye movements (see Andersen, 1989 for review). Cells with responses during hand actions have been found to code the features of objects (Sakata *et al.*, 1995; Murata *et al.*, 1996) and their orientation (e.g. Sakata *et al.*, 1997, 1998) and such neurones may be involved in matching hand movements to the spatial characteristics of objects. On the basis of the neurophysiology, it has been suggested (Sakata *et al.*, 1997) that the dorsal stream may be further divided into two pathways with one system subserving motion vision and the other subserving the perception of spatial position and the features of objects for the control of hand action.

Two recent studies support further the claim for form and spatial sensitivity in both dorsal and ventral cortical visual streams. Dobbins *et al.* (1998) reported distance-dependent changes in neural response to visual stimuli in V4 of macaque. Area V4 is at an intermediate level in the ventral visual pathway, and such effects were independent of retinal image size. Sereno and Maunsell (1998) recorded from neurones in the lateral intraparietal area (LIP) of the posterior parietal cortex of macaques. In a fixation task, they found selectivity for simple 2-dimensional shapes equivalent to the shape selectivity observed in areas of the ventral pathway (e.g. inferotemporal cortex). Additionally, in the delay period of a delayed matching-to-sample task, they observed shape selective delay activity similar to that found in

inferior temporal cortex and prefrontal cortex (e.g. Desimone, 1996). In contrast to most previous studies in parietal cortex, shape selectivity was observed even though the subjects were not required to manipulate or grasp objects (see also Sakata *et al.*, 1995). The posterior parietal cortex has been implicated in visuospatial attention and the shape selectivity observed may be related to attentional or intentional shifts to objects (Logothetis, 1998).

The status of STS with regard to the two cortical visual streams is not entirely clear. The anterior superior temporal sulcus has generally been considered part of the ventral stream although topological analysis has suggested that the upper bank of STS represents an area of reconvergence of the two streams (Young, 1992). In contrast, the caudal areas of STS including MST and FST are more associated with the dorsal stream and are often regarded as part of the parietal cortex. Anatomically, STS has been proposed to represent part of a third visual stream for visual motion analysis (Boussaoud *et al.*, 1990 - see section 2.4.1).

2.3 Frames of reference and the visual streams

Frames of reference provide the basis for specifying the spatial relationships between objects (e.g. Brewer and Pears, 1993). The position of an object in space can be coded with respect to the observer (egocentric reference frame) or with respect to other objects in the environment independent of the observer (allocentric reference frame). In terms of behaviour different frames of reference may be suited for different functions (e.g. Milner and Goodale, 1995, p. 88) and it is clear that there are multiple representations of space in different brain areas (for brief reviews see Rizzolatti *et al.*, 1994; Colby, 1998). An egocentric reference frame is suitable for

situations in which the organism is acting directly on the environment e.g. reaching out to touch an object. The important spatial information required for such an action is the position of the object relative to the organism. For navigation around the environment, however, an allocentric reference framework, independent of the observer is more appropriate. Here the important information is the relative positions of different objects within the environment enabling the observer to locate themselves or particular objects within that environment from any viewpoint. In this case, the coding of position remains constant despite changes in the location of the observer.

The hippocampus has been suggested as a site for the storage of allocentric spatial information (O'Keefe and Nadel, 1978 - see chapter 8). Neurones within the rat and primate hippocampus ("place cells") show responses related to the position of the animal within the environment (e.g. O'Keefe, 1979; Ono *et al.*, 1993). Experiments in the rat (e.g. O'Keefe and Conway, 1978) have shown that the responses of such place cells are determined by multiple distal visual cues. A population of neurones in the primate hippocampus have also been reported to be responsive to where the monkey is looking in the environment regardless of the position of the monkey or the monkey's head direction (e.g. Rolls *et al.*, 1997).

In the primate hippocampus, neurones responding to objects or movements at a particular spatial location have been found to respond in an allocentric manner (e.g. Tamura *et al.*, 1990, 1992; Feigenbaum and Rolls, 1991). Two forms of allocentric coding have been observed (Feigenbaum and Rolls, 1991). For some neurones, the frame of reference was found to be centred on the environment (e.g. Tamura *et al.*, 1990, 1992; Feigenbaum and Rolls, 1991). When the monkey was moved or rotated the area of sensitivity remained at the same location within the testing room. For

other neurones the frame of reference was found to be centred on the computer monitor used to display stimuli (Feigenbaum and Rolls, 1991). The relative position of the monitor with respect to the environment, and the monkey with respect to the monitor, were unimportant in determining the firing of such cells. These cells responded to stimuli presented at a particular location with respect to the sides of the monitor and can also be described as responding in an object-centred framework (see also section 2.4.2b).

Neurones responding in an object-centred manner have also been reported in the supplementary eye fields of the frontal cortex of macaque (Olson and Gettner, 1995). Such neurones responded strongly during eye movements directed to one end of a bar, but responded much less strongly during eye movements to the other end even if identical eye movements were required. The frame of reference seems to be centred on the object in question, not on the observer or external cues.

Egocentric coding implies that the frame of reference is centred on the observer's body, but many different egocentric frameworks are possible. The framework could be centred on the observer's eye forming an oculocentric map of space, or on other parts of the observer's body e.g. head, body or limb. In each case the framework can provide information on the spatial position of objects with respect to the body part (i.e. eye, head, body or limb) and this may reflect the different functions subserved (e.g. Fogassi *et al.*, 1996; Graziano and Gross, 1998). For example, cells in the ventral premotor cortex (area F4 of Rizzolatti and colleagues – see Matelli *et al.*, 1985) have been found to code spatial position in arm- and head-centred co-ordinates (Graziano *et al.*, 1994; Graziano and Gross, 1998). Many cells in this region are bimodal responding to visual and tactile stimuli and the visual receptive fields are commonly found to extend outward from the tactile receptive

fields (Fogassi *et al.*, 1996; Graziano *et al.*, 1997b). When the arm or head is moved, the visual receptive fields move correspondingly, independent of eye position (Graziano *et al.*, 1994; see also Fogassi *et al.*, 1996). Such a co-ordinate system may be useful for hand-eye co-ordination and for moving the head towards or away from nearby stimuli (Graziano and Gross, 1998).

In contrast, neurones in areas involved in the control of eye movements code space in retino- or oculo-centric co-ordinates with visual, auditory and somatosensory receptive fields that move with the eye (e.g. Groh and Sparks, 1996; Russo and Bruce, 1996).

The distinction between egocentric and allocentric processing may be mapped onto the two cortical visual streams. Contrary to the Ungerleider and Mishkin (1982) model, Milner and Goodale (Goodale and Milner 1992; Milner and Goodale, 1993, 1995) have suggested that spatial information may be required for both object/scene recognition and visuomotor function and may therefore be processed in both visual streams. The nature of the spatial information, however, may be different. Neurones in the dorsal stream involved in the production of eye movements and reaching and grasping respond in an egocentric framework. It may be that the dorsal stream ,because of its involvement in visuomotor function, is exclusively involved in the egocentric processing of space. Indeed, Milner and Goodale have stated (Milner and Goodale, 1995, p. 91) that if evidence for the allocentric coding of space is found within the dorsal stream, then that would favour the Ungerleider and Mishkin (1982) model over their own. In contrast the ventral stream may be involved in the processing of allocentric spatial information, which is dependent on the recognition of external visual cues.

Recently, Dijkerman *et al.* (1998) tested patient DF (see section 2.2) on a visuomotor task designed to force the use of allocentric processing. DF was presented with discs containing two or three holes and asked to reach out and place her fingers in the holes. It was argued that successful performance on the task requires the coding of the relative spatial positions of the holes i.e. allocentric coding. Although her hand orientation and localization (with respect to the disk) were often accurate when presented with a disc with two holes, she was completely unable to correctly adjust her grip aperture. In reaching for discs with three holes, she was impaired on all aspects of performance. Assuming that DF has a damaged ventral stream, these results support the notion of different spatial frames of reference operating in the two separate streams of cortical processing.

2.4 Superior temporal sulcus

The superior temporal sulcus (STS) in the macaque lies largely within the temporal lobe with the more caudal aspects adjacent to area PG in the parietal lobe and including areas MST, FST and parts of MT. Dorsal to the sulcus is the superior temporal gyrus with the inferior temporal gyrus located ventrally (Seltzer and Pandya, 1978). The more anterior region of the sulcus, located within the temporal lobe, is generally associated with the ventral stream. In this section I will principally focus on this anterior region, reviewing the anatomy, connections and neurophysiology.

2.4.1 Connections and anatomy

Anatomically, STS has been divided into several distinct areas, with the lower bank more associated with inferior temporal (IT) cortex. The terminology surrounding the different areas is heterogeneous and in this section I will give an overview of how the temporal lobe and in particular STS has been divided and the principal nomenclatures used.

On the basis of the connectivity of the cerebral cortex, Felleman and Van Essen (1991) divided the temporal lobe into 3 broad areas:

(1) Inferior temporal cortex consisting of the dorsal and ventral areas of PIT, CIT and AIT (posterior, central and anterior inferior temporal cortex respectively - including areas TE_{1-3}, TEa and TEm of Seltzer and Pandya, 1978; see below)

(2) Upper bank of STS (including areas TAa, TPO and PGa of Seltzer and Pandya, 1978) - often referred to as STP (or superior temporal polysensory area - see section 2.4.2a).

(3) Medial area, including the parahippocampal gyrus (areas TF and TH)

The dorsal areas of the regions of the inferior temporal cortex lie within the lower bank of STS. Felleman and Van Essen (1991) further divided the upper bank of STS into posterior and anterior superior temporal polysensory areas (STPp and STPa respectively).

The division of the upper bank of STS proposed by Seltzer and Pandya (1978), corresponds to longitudinal strips running along the length of the sulcus (see figure 2.1). Areas PGa, TPO and TAa (medial to lateral) all lie within the upper bank. A further strip, IPa, lies in the floor (or fundus) of the sulcus and extends slightly into

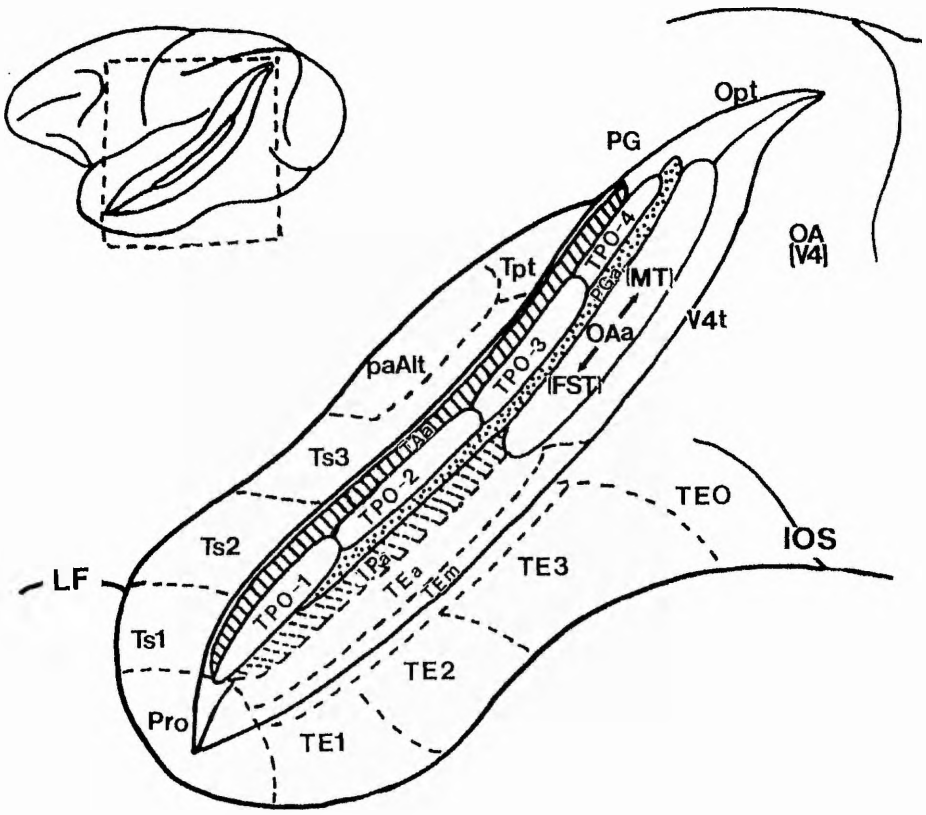


Figure 2.1 Top: Lateral view of the cerebral hemisphere of macaque showing the location of STS with the upper bank, lower bank, and fundus shown. Bottom: Enlargement of temporal lobe showing architectonic parcellation of STS and surrounding cortex. Areas TAa, TPO (1-4), PGa, IPa, TEa and TEm all lie within STS (from Seltzer and Pandya, 1994).

the lower bank. Figure 2.2 shows a series of coronal sections along the length of the sulcus with the relative positions of these areas labelled.

The lower bank of the sulcus extending round the inferior temporal gyrus to the occipitotemporal sulcus was considered one architectonic area by von Bonin and Bailey (1947) and termed TE. Following this terminology, Seltzer and Pandya (1978) defined several distinct areas TE_{1-3}, TEm and TEa. TEa is located entirely within the lower bank of STS with TEm more lateral on the edge of the sulcus.

The connections of the cortex of STS are polymodal and heterogeneous along its length. In particular, area TPO may be further divided into at least three different areas along its rostro-caudal length (Seltzer and Pandya 1989a, b, 1994, Cusick *et al.*, 1995). For example the nature of projections to and from the posterior parietal cortex (Seltzer and Pandya, 1984; Harries and Perrett, 1991) and to and from the frontal cortex (Seltzer and Pandya, 1989a) vary in density with rostro-caudal distance along the sulcus.

Recent anatomical studies have implicated anterior regions of STS as a potential site for the integration of spatial, motion and object information (Boussaoud *et al.*, 1990; Morel and Bullier, 1990; Baizer *et al.*, 1991). MST and FST located in the posterior parts of STS both project to anterior regions of STP (Boussaoud *et al.*, 1990) and both are known as sites for motion analysis (e.g. Desimone and Ungerleider, 1986). In analysis of the inputs to the dorsal and ventral cortical streams, Baizer *et al.* (1991), found that only two areas, V4 and the anterior regions of STS, project to both inferior temporal cortex and posterior parietal cortex. Additionally anterograde analysis in one subject showed that there were converging projections from the posterior parietal cortex and inferior temporal cortex to one site only: STS. The label from the parietal injection was found to be concentrated in the

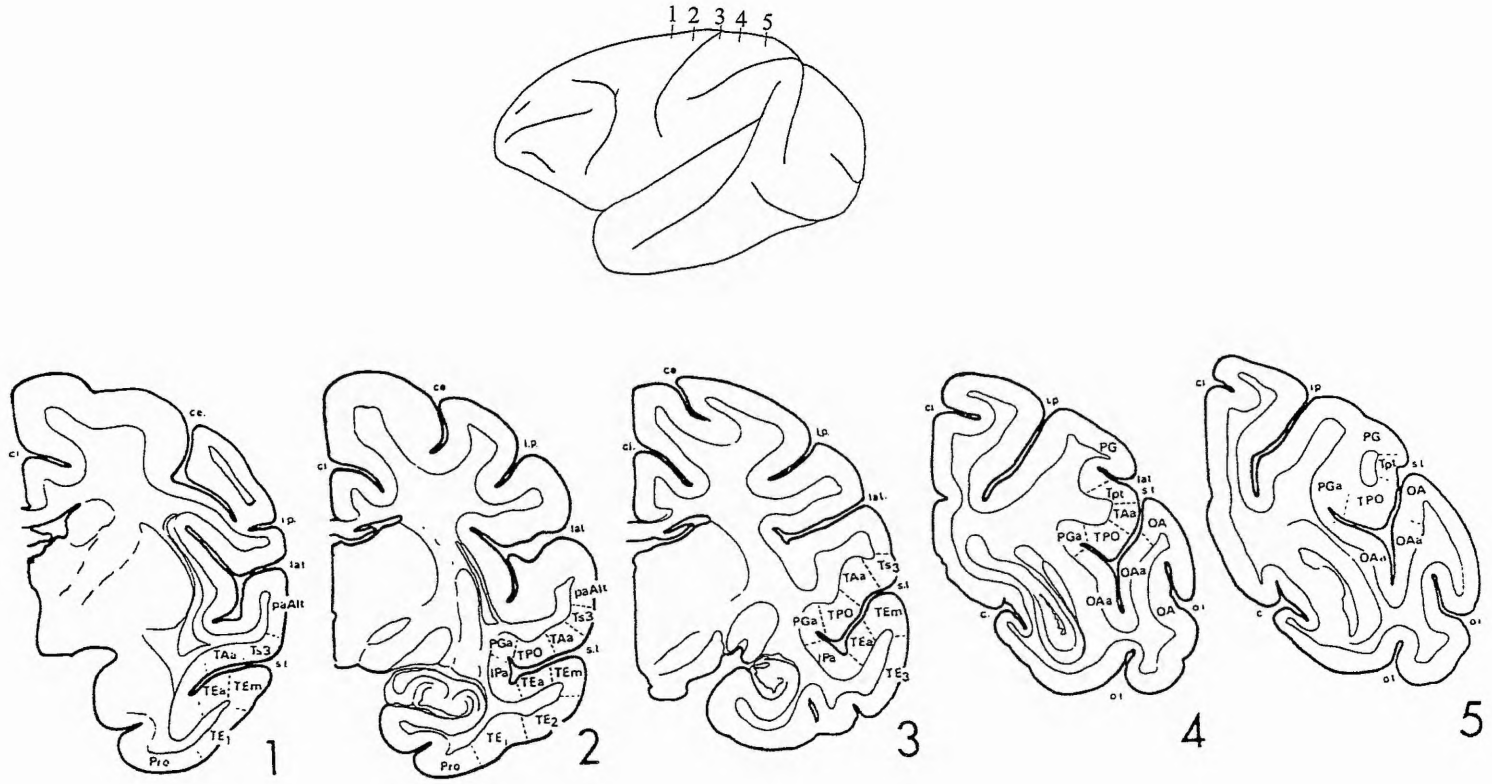


Figure 2.2 Coronal sections of the cerebral hemisphere of a macaque, taken at levels 1-5 indicated in the upper diagram, illustrating the architectonic parcellation of STS and surrounding cortex. Abbreviations: c., calcarine sulcus; c.e., central sulcus; c.i. cingulate sulcus; lat., lateral sulcus; o.i. occipitoinferior sulcus; o.t., occipitotemporal sulcus; s.t., superior temporal sulcus (adapted from Seltzer and Pandya, 1978).

upper bank, whereas the label from the temporal injection was found in the lower bank. The sites were found to overlap in the floor of the sulcus (corresponding to area IPa) at more anterior locations. It has been suggested that STSa may be part of a third stream of visual processing (Boussaoud *et al.*, 1990) involved in motion analysis. It represents a "multimodal zone of the multimodal zones", given its major sources of inputs from multimodal areas of the inferior parietal lobule and parahippocampal gyrus (Seltzer and Pandya, 1989b).

2.4.2 Neurophysiology

(a) General properties

Although STS has been divided on the basis of anatomy, the distinctions are much less clear in terms of the neurophysiology. The major distinction is between the upper and lower banks of the sulcus, but in many cases even this dichotomy is not clear. One of the principal findings has been the presence of cells selectively responsive to faces (e.g. Perrett *et al.*, 1982; Desimone *et al.*, 1984).

Desimone and Gross (1979) distinguished a polysensory area in the fundus and upper bank of STS, terming it STP (superior temporal polysensory area). This area probably corresponds to areas TPO and PGa (Cusick *et al.*, 1995). Most neurones in this area are visually responsive with more than half responding to more than one modality (Bruce *et al*, 1981). Vision has been regarded as the dominant modality and consequently most neurophysiological studies have focused on the visual responses only of neurones in this area.

In contrast, the lower bank of the sulcus has been regarded as predominantly a unimodal visual area (e.g. Baylis *et al.*, 1987). Benevento *et al.* (1977), however, recorded auditory and visual responses in anterior regions of the sulcus and made no distinction between the upper and lower banks.

Recording from all the principal divisions of the temporal cortex as defined by Seltzer and Pandya (1978), Baylis *et al.* (1987) attempted to correlate functional and anatomical areas. Cells in TAa were influenced by visual and auditory stimuli; TPO, PGa and IPa by visual, auditory and somatosensory stimuli; and TE_{1-3}, TEa and TEm primarily by visual stimuli. Many neurones in areas TPO, PGa and IPa responded to moving stimuli, similar to earlier reports (Bruce *et al.*, 1981). In contrast, few neurones in areas TE_{1-3}, TEa and TEm responded to motion. Neurones responsive to faces were found predominantly in areas TPO, TEa and TEm and neurones that responded to complex visual stimuli only (excluding faces) were common in areas TE_1, TE_3 and TEm. Cells responsive to faces, however, have been reported in areas TE_{1-3} (Tanaka *et al.*, 1991). Table 2.1 summarises the principal characteristics of cells in areas of the temporal cortex.

Physiologically, as anatomically, rostro-caudal divisions of STS are evident. In the caudal areas of STS (MT, MST and FST), there is a predominant responsiveness to visual motion with neurones in MST showing responses related to eye movements and in particular, smooth visual pursuit (e.g. Desimone and Ungerleider, 1986; Newsome *et al.*, 1988). Recording in caudal areas of STP, including MST, Hikosaka *et al.* (1988) reported polysensory properties distinct from those in more rostral areas. In particular, the incidence of multimodal neurones and visual responsiveness was much less in caudal STP than rostral STP.

Area of cortex	Divisions of Seltzer and Pandya (1978)	Principal modalities of responsiveness	Cells selective for faces	Cells sensitive to motion
Upper bank of STS	TAa	Visual and auditory	×	✓
	TPO	Visual, auditory and somatosensory	✓	✓
	PGa	Visual, auditory and somatosensory	few	✓
Floor of STS	IPa	Visual, auditory and somatosensory	few	✓
Lower bank of STS	TEa	Visual	✓	×
	TEm	Visual	✓	×
Inferior temporal cortex	TE_{1-3}	Visual	few	×

Table 2.1. Summary of the principal characteristics of cells in the banks of STS and in inferior temporal cortex.

The receptive fields of neurones in IT cortex are large, often bilateral and always include the fovea (e.g. Richmond *et al.*, 1983; Gross *et al.*, 1972). In anterior IT, the receptive fields are found to be larger than posterior IT (Tanaka *et al.*, 1991; Hikosaka, 1998) and the nature of effective stimuli also changes. In posterior IT most cells will fire in response to simple stimuli such as bars or discs, whereas in anterior regions, more complex features are often required (Tanaka *et al.*, 1991; Kobatake and Tanaka, 1994). The somatic and visual receptive fields of neurones in the anterior portion of STP often include the whole body or whole visual field (e.g. Bruce *et al.*, 1981; Mistlin and Perrett, 1990) whereas those in more posterior regions tend to be more circumscribed (e.g. Hikosaka *et al.*, 1988). In comparison with IT cortex, the receptive fields in STP are much larger, more often bilateral and show uniform responses across the whole receptive field (Bruce *et al.*, 1981).

Neurones responsive to the sight of monkey and human faces have been reported in both upper and lower banks of STS and in other regions of IT cortex (e.g. Bruce *et al.*, 1981; Perrett *et al.*, 1982; Desimone *et al.*, 1984; Rolls, 1984; Baylis *et al.*, 1985; Yamane *et al.*, 1988; Oram and Perrett, 1992; Perrett *et al.*, 1992). Such cells have been described as face-selective given their lack of responsiveness to other simple and complex visual stimuli (including jumbled faces) and the failure to elicit responses with other non-specific arousing tactile, visual and auditory stimuli (e.g. Perrett *et al.*, 1982; Desimone *et al.*, 1984). The majority of these neurones show view selectivity, responding preferentially to particular views of the head with selectivity for the four characteristic views (front, left profile, right profile and back) more commonly encountered (Perrett *et al.*, 1991). Cells have also been found responsive to bodies and body parts e.g. hands (e.g. Desimone *et al.*, 1984; Wachsmuth *et al.*, 1994)

Very few cells are found with selectivity for identity (e.g. Perrett *et al.*, 1984), although facial identity could be encoded in an ensemble of neurones (Baylis *et al.*, 1985). Cells have been reported, however, responsive to facial expression (e.g. Perrett *et al.*, 1984; Hasselmo *et al.*, 1989; Perrett and Mistlin, 1990). For example, the cell illustrated in figure 2.3 showed a much greater response to a yawning expression than to a neutral expression or a threat expression (with similar opening of the mouth) for both front and profile views of the head. Cells responsive to faces in STS may therefore be involved more in social cognition than recognition of identity.

It has been suggested that a function of the view-selective cells may be to code the direction of attention of another individual (e.g. Perrett *et al.*, 1992). Such information is crucial for understanding the social signals (e.g. threat) of conspecifics and whether or not such signals are directed at you. In support of this view, cells have been reported with responses that can be modulated by gaze direction or that will respond to multiple configurations of head and body as long as attention is directed towards a particular location (e.g. Perrett *et al.*, 1985b; Perrett *et al.*, 1991; Perrett *et al.*, 1992). Figure 2.4a, b shows the responses of one cell that could be characterised as responding to "gaze down". The cell responded more to the head pointing down than head level (figure 2.4a). The response to head level was further modulated by the direction of gaze such that the response to gaze down was significantly greater than the response to gaze level or gaze up. Body posture was also an important cue (figure 2.4b). With the head occluded there was a greater response to a quadrupedal posture (in which the direction of attention would appear to be down) than to the bipedal posture. With the head visible, the response to the quadrupedal posture was further modulated by the head angle such that the response

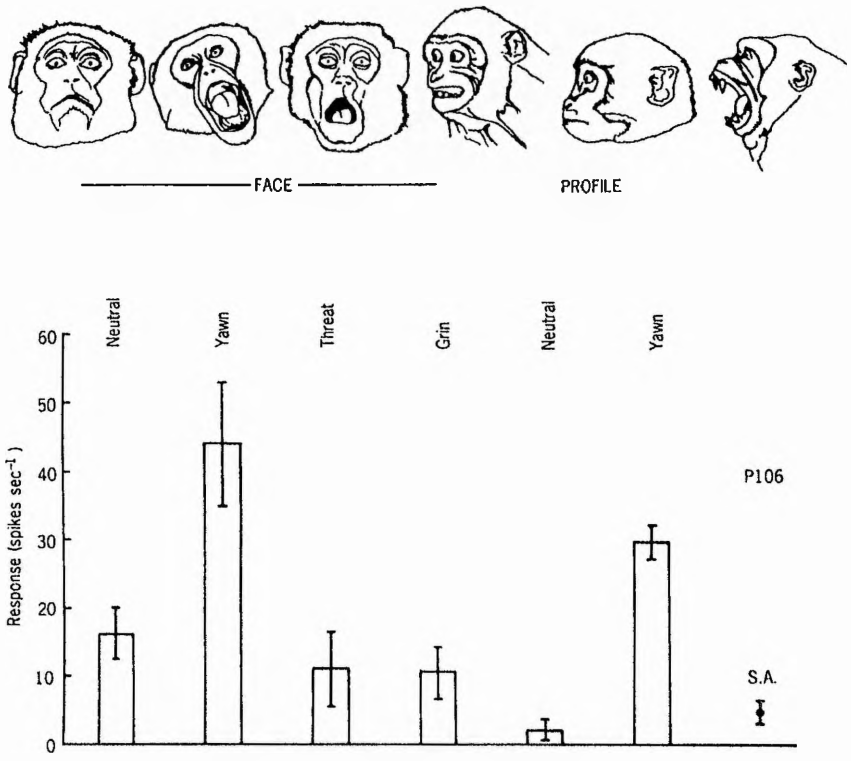


Figure 2.3 Responses of a cell in STSa to different facial expressions displayed in two views of a macaque. The cell showed greater responses to a yawn expression than to a neutral or a threat expression (with equivalent opening of the mouth) for both views tested (from Perrett and Mistlin, 1990).

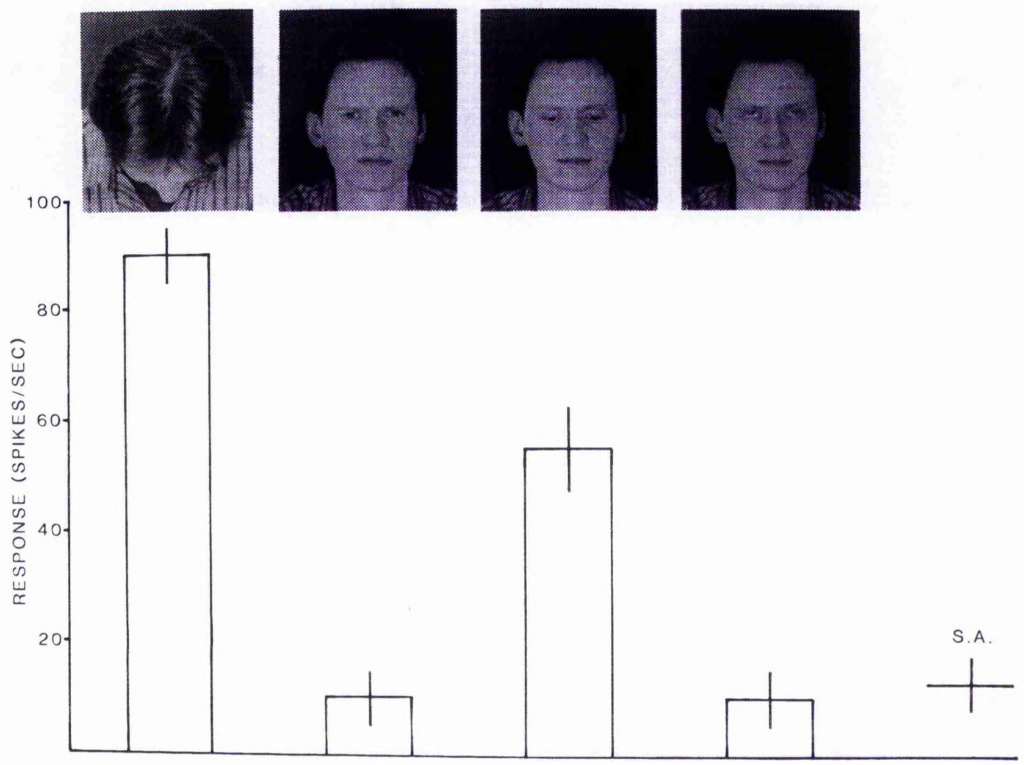


Figure 2.4a Responses of a cell in STSa (+/- standard error) showing modulation of activity with gaze direction. The cell showed a significantly greater response to a downturned head than to an upright head. Furthermore, the cell showed modulation of the response to the upright head depending on eye position. The response to eyes directed down was significantly greater than the response to eyes level or eyes up. S.A. = spontaneous activity. (from Perrett *et al.*, 1992).

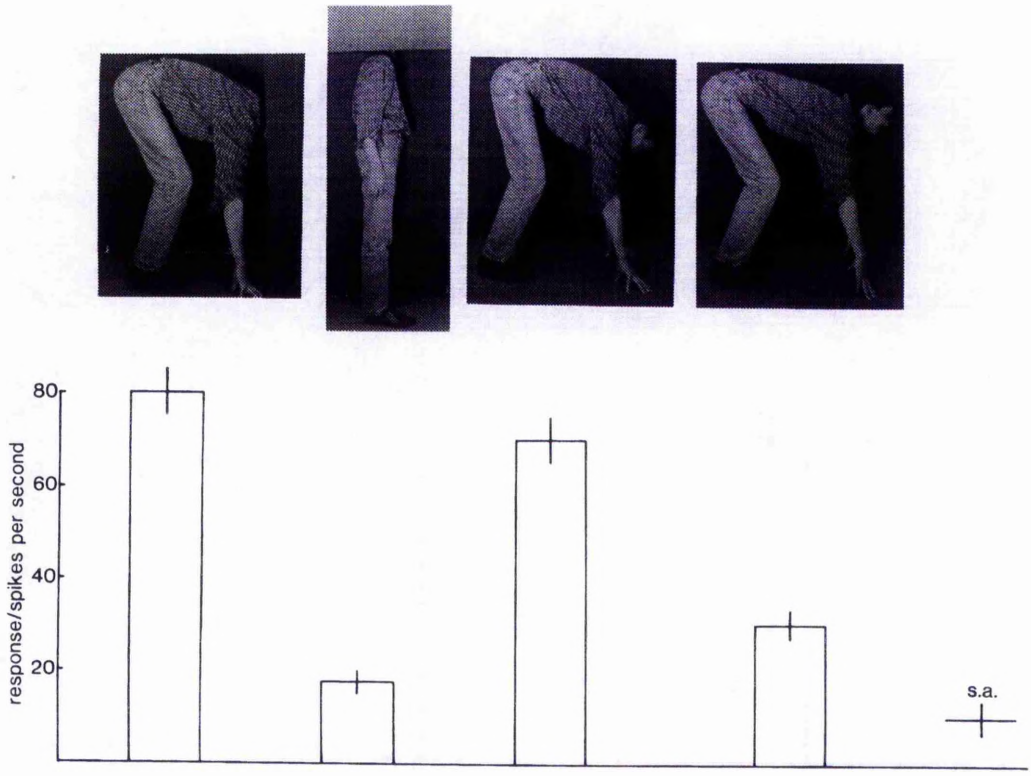


Figure 2.4b Responses of the same cell as figure 2.3a to different postural positions. The cell showed greatest responses to postures in which the visual evidence suggested that the direction of attention was down. Conventions are the same as figure 2.4a. (from Perrett *et al.*, 1992).

to head down was significantly greater than that to head up. In summary, the sensitivity of this cell to each visual cue is consistent with coding of attention direction.

In caudal regions of STS, cells in areas MT, MST and FST show responses principally related to the processing of visual movement. Studies in more rostral areas of STS also show movement sensitivity and responses to complex body movements such as walking and limb articulation have been reported (e.g. Perrett *et al.*, 1985, 1990). Such responses show integration of form and motion information (Oram and Perrett, 1994) probably with direct input from MST and FST (Boussaoud *et al.*, 1990).

In the lower bank of STS (corresponding to area TEa), Perrett *et al.* (1989) reported cells responsive to hand-object interactions. Such cells responded differentially to different hand actions (e.g. manipulate, present, pick, tear) and the majority showed generalisation of response across multiple viewing conditions.

In summary, the response characteristics of cells in STS are heterogeneous. Cells are found responsive to faces, bodies and complex body movements and STS may play a critical role in social cognition (Emery and Perrett, 1994; Emery, 1997). As you move from the posterior to the anterior end of the sulcus, the size of the receptive fields and the complexity of visual stimuli required to elicit responses increases.

(b) Frames of reference in STS

Responses of cells in STSa have been classified as responding in three different co-ordinate frames: viewer-centred, object-centred, and goal-centred (e.g.

Perrett *et al.*, 1989; Perrett *et al.*, 1990). In this section I will define what is meant by each of these co-ordinate frames and relate them to the ego- and allo-centric spatial reference frames previously described.

(i) Viewer-centred

Most cells reported respond in a viewer-centred manner, that is, the cells are responsive to a particular object view with respect to the subject. The distance from the subject, size of image and the retinal position are relatively unimportant (Perrett *et al.*, 1982; Desimone *et al.*, 1984; Rolls and Baylis, 1986)). This is an egocentric representation. It should be noted, however, that such coding has rarely been studied in a systematic way. Tests that could exclude or demonstrate an allocentric influence (e.g. moving the monkey) have often not been performed.

(ii) Object-centred

A much smaller number of cells have been found to respond in a object-centred manner (Perrett *et al.*, 1985; Perrett *et al.*, 1991). These cells show complicated response patterns that are very difficult to understand and interpret in viewer-centred terms. For example, the cell illustrated in figure 2.5 (Perrett *et al.*, 1990, 1991) showed significant responses (relative to spontaneous activity) to a laterally extended arm rotated to the front when the experimenter was facing the subject. Movement of either arm was effective. In this case, the arm movements were directed towards the subject. When the experimenter was facing in the opposite direction, however, the cell responded to equivalent movements of the arms directed away from the subject. In viewer-centred terms this response pattern does not make sense. The nature of the movements is the same, however, with respect to the

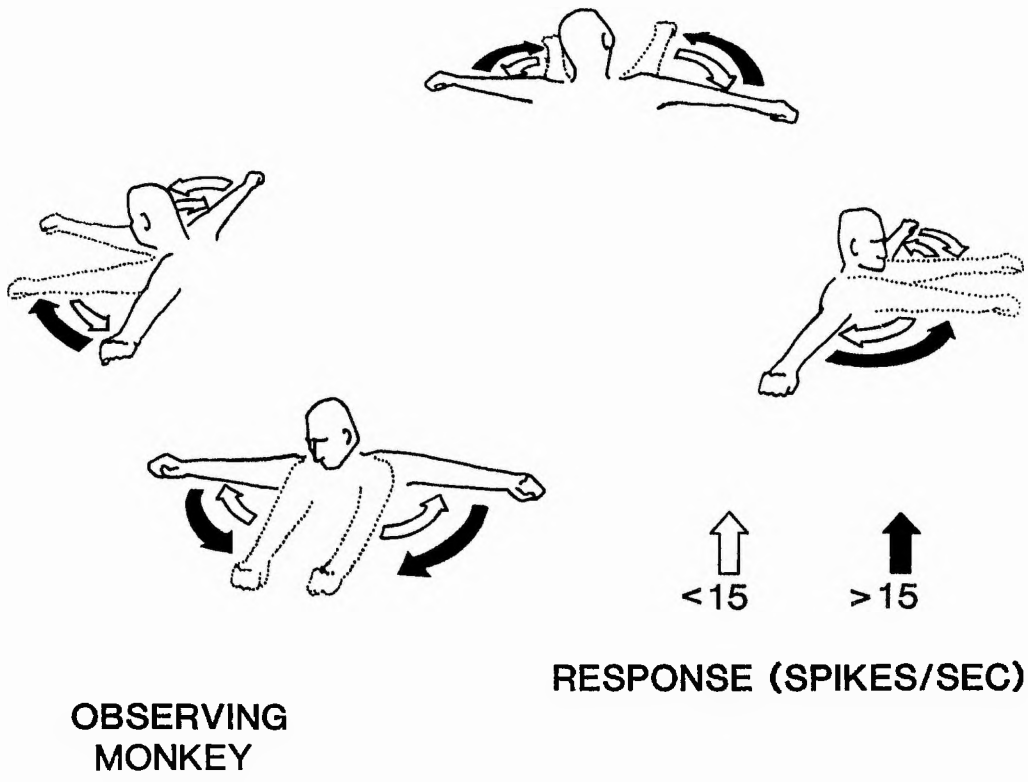


Figure 2.5 Responses of a cell showing object-centred coding. The cell showed greatest responses to movement of the arms from a laterally extended position to the front of the experimenter for all views. The cell responded to movement of the arms with respect to the experimenter and was not responding in a viewer-centred manner (from Perrett *et al.*, 1989).

experimenter - "bringing hands to the front of the experimenter". The cell also responded to the same movements when the experimenter was facing either left or right (the reduced response to the movement of the furthest arm when the experimenter was in profile may reflect the partial occlusion of the arm by the body - Perrett *et al.*, 1990). It appears that the cell is responding to the movements relative to the experimenter (i.e. with a frame of reference centred on the experimenter).

Object-centred coding amounts to a generalisation across perspective view (Perrett *et al.*, 1991) and cells responsive to multiple views of static objects (e.g. heads) may be interpreted as object-centred. Such properties could result from the pooling of responses from cells responsive to individual views. Cells responsive to multiple views of moving stimuli (Perrett *et al.*, 1985), for example responding to a person walking in any direction as long as they are facing the direction of movement, may also be interpreted as object-centred (Perrett *et al.*, 1990). Such responses require a combination of view and direction of movement (e.g. view left, move left or view right, move right, but not view right, move left or view left, move right) and cannot result from a simple pooling of view or direction selective cells. These cells could operate by combining the responses from cells sensitive to body view *and* direction (e.g. view left, move left + view right, move right + view forward, move forward + view back, move away).

Coding in an object-centred manner can be regarded as a form of allocentric coding. The frame of reference for the object or movement is external to the observer and based on the object itself.

(iii) Goal-centred

For goal-centred coding, the frame of reference is centred on an object or position external to the observer and the object of interest. The cell illustrated in figure 2.6 shows an example of goal-centred coding. This cell responded to whole body movement, but only when that body movement was directed towards one of the doors of the testing room. The direction of movement was unimportant and the same pattern of responses was observed when the monkey's view was changed by rotating the primate chair. The responses of the cell are clearly not viewer-centred or object-centred. Instead the frame of reference appears to be the layout of the room and in particular the location of the door. The door can be viewed as the "goal" which whole body movements may attain. Any movements that lead to the goal produce a response from the cell.

Further examples of goal-centred coding have been seen in cells responsive to reaching movements of the arms (Perrett *et al.*, 1989). These cells only responded when the reaching movement brought the experimenter's arm to a particular location in space where a target object may have been situated. In this case the goal can be seen as the object or spatial location.

Cells responsive to hand-object interactions also show evidence of goal-centred coding (e.g. Perrett *et al.*, 1989). The cells were found to be unresponsive to the hand movements alone, the object movements alone or the hand and object movements performed concurrently but with a spatial separation between the two. Thus the cells are responsive to hand actions in relation to a goal (object manipulated).

For the responses of the cells described above, the spatial relationship between the object (e.g. experimenter) and goal (which may itself be a spatial

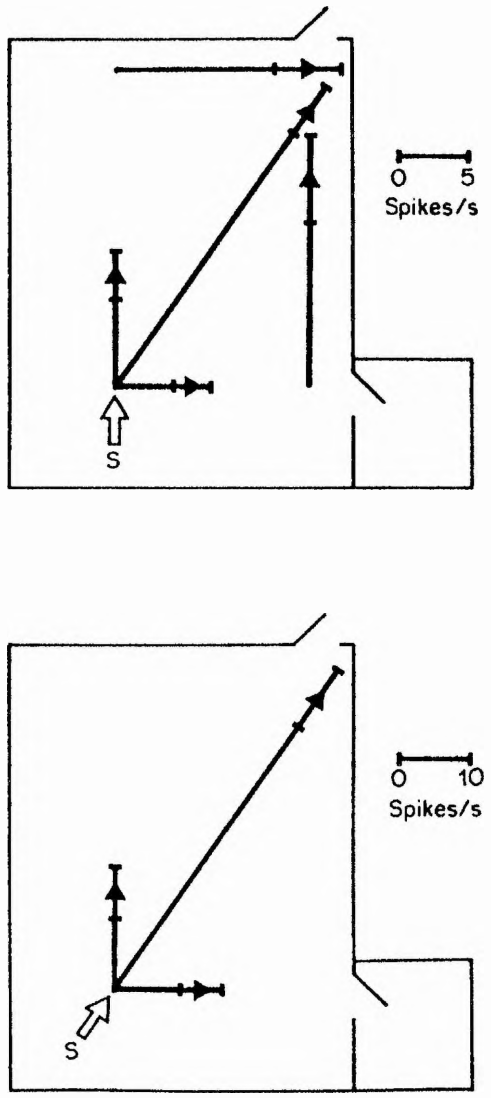


Figure 2.6 Responses of a cell showing goal-centred coding. The cell responded to movement of the experimenter in the direction of one of the doors to the room (the goal - top right). The direction of movement was unimportant as long as it led to the door. Equivalent movements that did not lead to the door were ineffective. The responses were the same regardless of the orientation of the monkey (top versus bottom). S = monkey subject (from Perrett *et al.*, 1991).

position) is critical. Goal-centred coding is another form of allocentric coding. The frame of reference is centred on the goal in question, which is external to the observer. Unlike viewer and object-centred coding, goal-centred coding may operate on a spatial framework. The relative spatial positions of the experimenter and the goal (an object or a position) determine the firing responses of the cells.

2.5 SUMMARY

Visual processing in the cortex is thought to proceed in two separate pathways: the dorsal stream for visuomotor processing and the ventral stream for object and scene recognition. Anterior regions of STS are generally associated with the ventral stream, although anatomical studies suggest that this area may be a site of reconvergence of the two visual streams. Cells in this region show responses to complex stimuli such as faces and body movements and may be important in social cognition. These responses appear to be encoded in both egocentric and allocentric reference frames and spatial position may be critical in determining the responses of some cells.

CHAPTER 3

OBJECT PERMANENCE

3.1 INTRODUCTION

If we place a ball in a box and close the lid, there is no direct perceptual evidence to suggest that the ball still exists. Yet, if we open the box, we would expect to find the ball exactly as before with the same size, colour and weight. Similarly if we turn the light off in a room, we expect the objects in that room and their spatial configuration to be still the same when we turn the light on again. Empirically, objects have an existence independent of observation. This applies both prospectively and retrospectively. If we walk into a room and turn the lights on, the objects that become visible are not perceived as having just come into existence, but as having had a prior existence. In our everyday environment, objects are continually moving into and out of sight, yet our experience is of a stable environment cluttered with persisting or "permanent" objects. As Piaget (1954) notes:

"A universe without objects.....is a world in which space does not constitute a solid environment.....it is a world of pictures each one of which can be known and analysed but which disappear and reappear capriciously"

Objects generally do not suddenly disappear or appear (even when out of sight), and the appeal of much stage magic is in the apparent violation of this principle (Michotte 1950, 1955).

Objects may move out of direct visual experience through the interposition of another object or through the elimination of light. The opposite events (i.e. the onset of light or the removal of an interposing object) bring objects into view. Throughout this thesis, I will use the term "occlusion" to refer to the disappearance of an object from view due to interposition (see Gibson *et al.*, 1969). An interposing object will be referred to as an "occluder". Interposition can occur through the movement of the occluder, the object or the observer.

3.2 Definitions of object permanence

"Object permanence" (e.g. Harris, 1989; Baillargeon, 1993), "existence constancy" (Bower, 1967; Gibson, 1979) and "object conservation" (Etienne, 1973) are terms that have been used to describe this phenomenon. The term existence constancy arises because object permanence can be ascribed as a constancy similar to perceptual constancies such as size constancy and brightness constancy (Michotte, 1950). For example, size constancy is the capacity to see an object as invariant under the transformation of change in retinal size. Brightness constancy is the capacity to see objects as invariant under the transformation of change in illumination or brightness. Similarly, object permanence can be viewed as the capacity to see objects as invariant under the transformations of appearance and disappearance. Throughout the text I will use the term object permanence, as this is the predominant term in the developmental (for example, see Harris, 1989; Baillargeon, 1993) and comparative psychological literature (for example, see Doré and Dumas, 1987). The term should be distinguished from "object constancy" which is a term that has been used to

describe a related phenomenon, that of the ability to recognise an object as the same structure from different viewing angles (Humphreys and Riddoch, 1984, 1985).

Table 3.1 summarises different definitions that have been given for object permanence. It can be seen from these definitions that object permanence has primarily been perceived as a problem in the visual domain. However, there is no reason why it should not apply to all other perceptual domains, for example, the tactile domain (Michotte, 1950). An object touched out of sight does not suddenly come into existence when we touch it.

It is also clear that object permanence has been taken to imply knowledge of the maintenance of stimulus characteristics. As described in the opening paragraph we expect a recovered hidden ball to have retained all of its physical properties. For example, we would expect the ball to be of the same size, shape and colour. Object permanence does not just entail representation of some entity that still exists but a specific object with defined characteristics. The series of assumptions that are involved in the concept of object permanence have been elaborated by Baillargeon (1993). These assumptions are:

(a) that the occluded object continues to exist behind the occluder

(b) that the occluded object retains the spatial and physical properties it possessed prior to occlusion

(c) that the occluded object is still subject to physical laws

Object permanence applies equally well to dynamic, mobile objects as well as static objects. In retaining its physical properties prior to occlusion, however, a mobile object may not retain its position.

Piaget (1954)	The conception and perception of "objects that have substance, that are permanent and of constant dimensions".
Michotte (1963)	"...the apparent continuity of the presence of an object and certain of its properties, including movement, in the face of modifications in the stimulus conditions and even the disappearance of the object from the visual field..."
Bower (1967)	"...our belief in the continued existence of objects which have disappeared and, complementarily, our belief in the preexistence of objects which have just appeared"
Butterworth (1991)	"...the experience that objects persist through space and time despite the fact that their presence in the visual field may be discontinuous"
de Blois, Novak and Bond (1998)	"The ability to represent the existence and movements of unperceived objects..."

Table 3.1. Examples of different definitions of object permanence.

3.3 OBJECT PERMANENCE SCALE

Object permanence has been extensively studied in development (for reviews see Bower, 1982; Harris, 1989; Spelke *et al.*, 1992; Baillargeon, 1993) since it is not evident in the behaviour of young infants. This is illustrated by the observations of William James (1890):

"A baby's rattle drops out of his hand but the baby looks not for it. It has gone out for him as a candle flame goes out and it comes back when relit. The idea of its being a thing whose permanent existence by itself he might interpolate between its successive apparitions, has evidently not occurred to him."

Based on observations of his own children, Piaget (1954) broke down the development of object permanence in humans into six stages. These stages, summarised in table 3.2, are based on infants' behaviour towards hidden objects. Initially infants do not track visually an object that moves out of their field of view. Similarly, they make no attempt to retrieve an object that has been covered over with a cloth even though the presence of the object is indicated by a distinct protuberance. Progressively infants' behaviour develops and by 8 months, hidden objects are no longer treated as if they cease to exist on occlusion.

The stage 4 infant (8-12 months) will reach for hidden objects but exhibits a characteristic error, referred to in table 3.2 as the perseveration error. It is also referred to as the "A not B error" (e.g. Harris, 1989; Wellman *et al.*, 1986; Ahmed and Ruffman, 1998). Stage 4 infants will recover an object hidden behind one of two occluders (e.g. occluder A), but fail when the hiding location of the object is changed

Stage	Description
1 and 2	No search for hidden objects. Infants stare at their point of disappearance.
3	Infants can retrieve a partly hidden object.
4a	Infants can retrieve a totally hidden object if they initiated search before the object was completely hidden.
4b	Infants can retrieve a totally hidden object, but they persist in searching a previously rewarded screen even if they saw the object disappear behind a new screen (perseveration error).
5a	Infants overcome the perseveration error, and they can find an object that was hidden behind a different screen on every trial.
5b	Infants can find an object that was hidden behind various screens within the same trial.
6a	Infants can find an object that was invisibly hidden behind a different screen on every trial.
6b	Infants can find an object that was invisibly hidden behind various screens within the same trial.

Table 3.2. Summary of Piaget's 6 stages of object permanence development (from de Blois, Novak and Bond, 1998)

from one occluder to the other (occluder B), searching under occluder A instead (see figure 3.1). They show perseveration of response, responding to the previously reinforced location. The exhibition of such an error is not dependent on the nature of the occluders and has been shown to occur even when the objects are placed into boxes with transparent lids (Butterworth, 1977). The length of delay between the hiding of the object and searching is critical. Human infants between 7.5 and 9 months succeed on the A not B task when there is no delay interposed between hiding and searching, but fail when a delay of only 1-5s is introduced (Diamond, 1985). The length of delay required for production of the error increases with age of the infant (Diamond, 1985; Wellman *et al.*, 1986; Ahmed and Ruffman, 1998). Often infants will look at the correct occluder even while reaching for the incorrect occluder (Diamond, 1988) and it has been suggested that the error may arise due to an inability to inhibit a prepotent response (Diamond and Goldman-Rakic, 1989).

Stages 5 and 6 of Piaget's scale are characterised by behaviour on visible (see figure 3.2) and invisible displacement (see figure 3.3) tasks. In a visible displacement task the object is first placed under one occluder and then in full sight of the infant, removed and placed under another occluder. Invisible displacement tasks are similar except that the movements of the object after the initial occlusion are concealed. For example, in an invisible displacement task, the object is first placed under an occluder (A), and then both object and occluder A placed under a second occluder (B). Here, the object is removed, out of sight of the infant, and the occluder A brought back into view. From an observer's point of view, the object could conceivably be under occluder A or occluder B, but infants less than 18 months fail on this task, searching only under the occluder where they saw the object disappear.

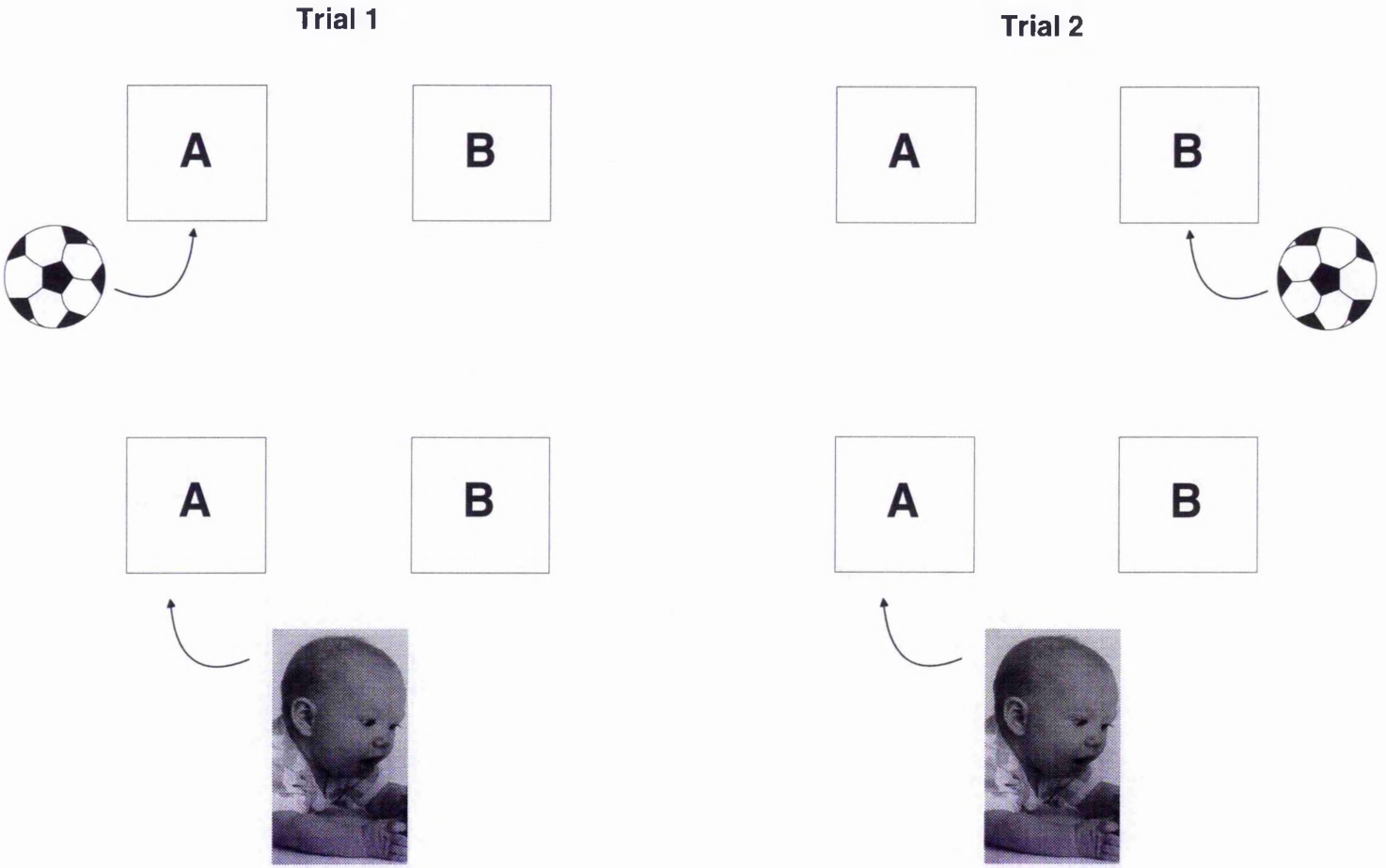
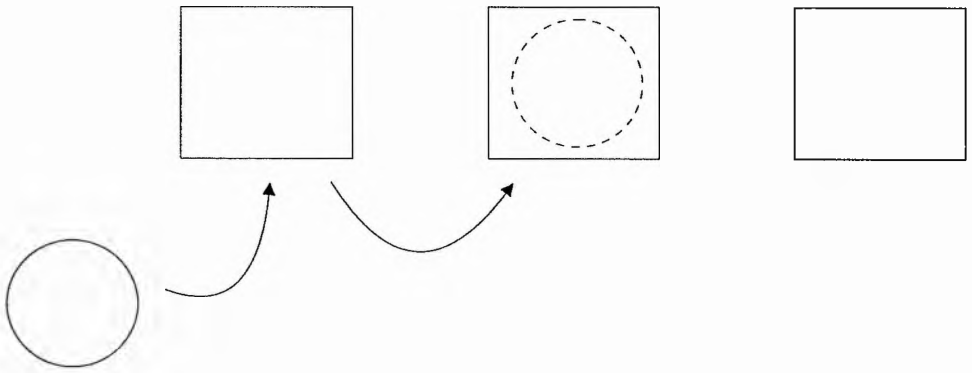


Figure 3.1 The A not B error. In trial 1 the object is hidden at A and the infant successfully searches at A. In trial 2, the object is hidden at B, but the infant searches again at A, the previously rewarded location.

Single visible displacement



Multiple visible displacement

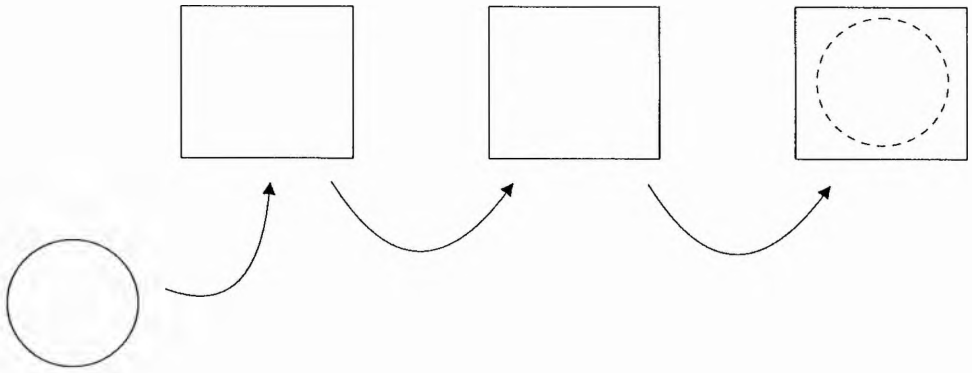
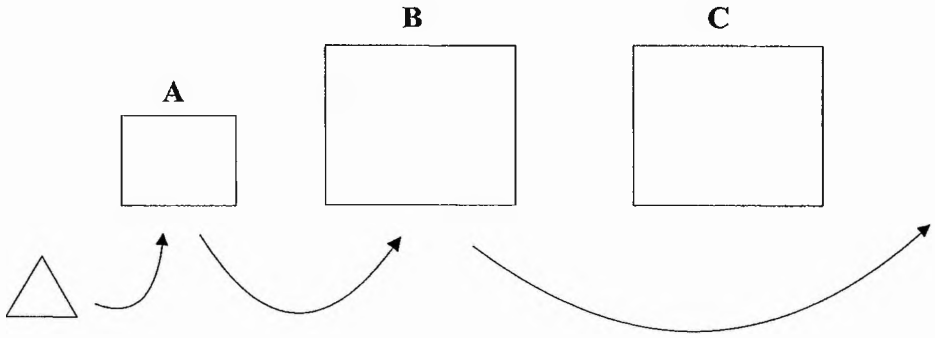


Figure 3.2 Top: single visible displacement task. The object is hidden under one occluder and then in full sight of the infant, removed and placed under a second occluder. The final position of the object is marked. Bottom: multiple visible displacement task. The object is hidden successively under several occluders (with the movements of the object always in view) before the infant is allowed to reach.

Sequence of events



Final position

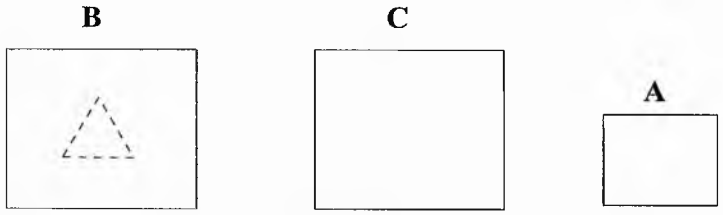


Figure 3.3 Invisible displacement. Top: sequence of events in an invisible displacement trial. The triangular object is first placed under the small occluder and both are placed under a second occluder. The triangular object is removed out of sight and the small occluder brought back into view. Bottom: final position of the occluders and the object.

Levels a and b of stages 5 and 6 differ in terms of the number of displacements that occur on a given trial. For level (a) only one displacement occurs per trial whereas for level (b) there are multiple displacements of the object before the infant is allowed to try and retrieve it. For example in a visible displacement task with multiple displacements (see figure 3.2), the object if first hidden under one occluder, and then under a second and third occluder in succession. All movements of the object are in full sight of the infant before the child is allowed to reach.

Success on invisible displacement tasks implies that the infant is able to represent the unseen movements of the object. Only when infants reached stage 6 of object permanence did Piaget (1954) consider full representational capacities to be present.

The sequence described by Piaget has received support from a number of large-scale replication studies in human infants (e.g. Décarie, 1965; Corman and Escalona, 1969; Uzgiris and Hunt, 1975).

3.4 Object permanence as a perceptual or conceptual issue

There is an apparent paradox to object permanence in that an occluded object and an annihilated object both present the same direct perceptual information.

"An occluded object ought to be indistinguishable from a destroyed object, whereas in fact it is distinguishable. A radical resolution of the paradox is to assume that the sensation of an object is *not* entailed in its perception; all that is required for perception is the colourless and formless information to specify a persisting object on the one hand or a destroyed object on the other." (Gibson *et al.*, 1969)

By this, Gibson *et al.* mean that the sensation of a persisting object does not derive from the immediately available perceptual evidence. Further information must be needed to distinguish a permanent object from a destroyed object. This information might derive from a perceptual or a conceptual level and Piaget and Michotte were in disagreement over the relationship and relative importance of the two levels (Butterworth, 1991).

Piaget reasoned that a child has to learn that an object out of sight has an independent existence. Occlusion events are common in any child's environment and through experience a child learns that an occluded object will still be there when the occluder is removed. This might be supplemented by evidence presented to the different senses. For example, an occluded object might not be visible, but it can still be experienced tactually, confirming its continued existence.

Michotte, on the other hand, argued that perception was dominant and that in the natural occlusion of objects, "the transformation itself is full of meaning" (Michotte, Piéron and Piaget, 1955 - quoted in Butterworth, 1991). For Michotte, sensory "impressions" could be regarded as an "actual prefiguration" of the basic concepts about the physical world (Michotte, 1950). Gibson *et al.* (1969) believed similarly:

"When the optical information is of one particular sort the persistence of an object is specified; when it is of another general sort the non-persistence of the object is specified. All the child has to do is distinguish the two general cases. Developmentally, he may have to learn to distinguish them but the development is one of perception, not of belief"

The "sorts" of optical information that lead to object permanence have been elaborated by both Michotte (1955; Bower, 1967) and Gibson (1979; Gibson *et al.*, 1969). Much research has focused on one of these stimulus conditions, that of gradual occlusion (and its counterpart gradual revealing). This is the stimulus configuration involved in interposition (the edge of one surface conceals another surface) and it has been termed the "screen effect" (Michotte, 1950; Michotte *et al.*, 1964). The progression of the stimulus configuration through time is shown diagrammatically in figure 3.4. The object moves towards the occluder and, upon reaching it, is gradually and incrementally occluded until the object is no longer in view. Stimulus conditions that fail to evoke object permanence include implosion and sudden disappearance (i.e. all parts of the object disappear simultaneously).

Examples of situations in which perceptual evidence overrides knowledge (e.g. magician's illusion of vanishing) have been given as evidence for the dominance of perception over cognition (Michotte, 1955). When the magician vanishes in a puff of smoke the overriding impression is of annihilation of the magician, consistent with the perceptual evidence. The observer knows, however, that this is impossible, that the magician still exists, and that they are simply witnessing a "trick".

Piaget suggested that the perception of object permanence would not be fully elaborated until the end of infancy at about 18 months, but more recent studies suggest that it may develop much earlier (e.g. Bower, 1967; Baillargeon *et al.*, 1985; Baillargeon, 1986, 1987; Hood and Willatts, 1986; see Baillargeon, 1993 for recent review) at a stage when the infant is unable to act to reverse the occlusion due to limited motor capabilities (see Bower and Wishart, 1972). Piagetian assessment relies on the manual capabilities of the infant, but these other studies have employed

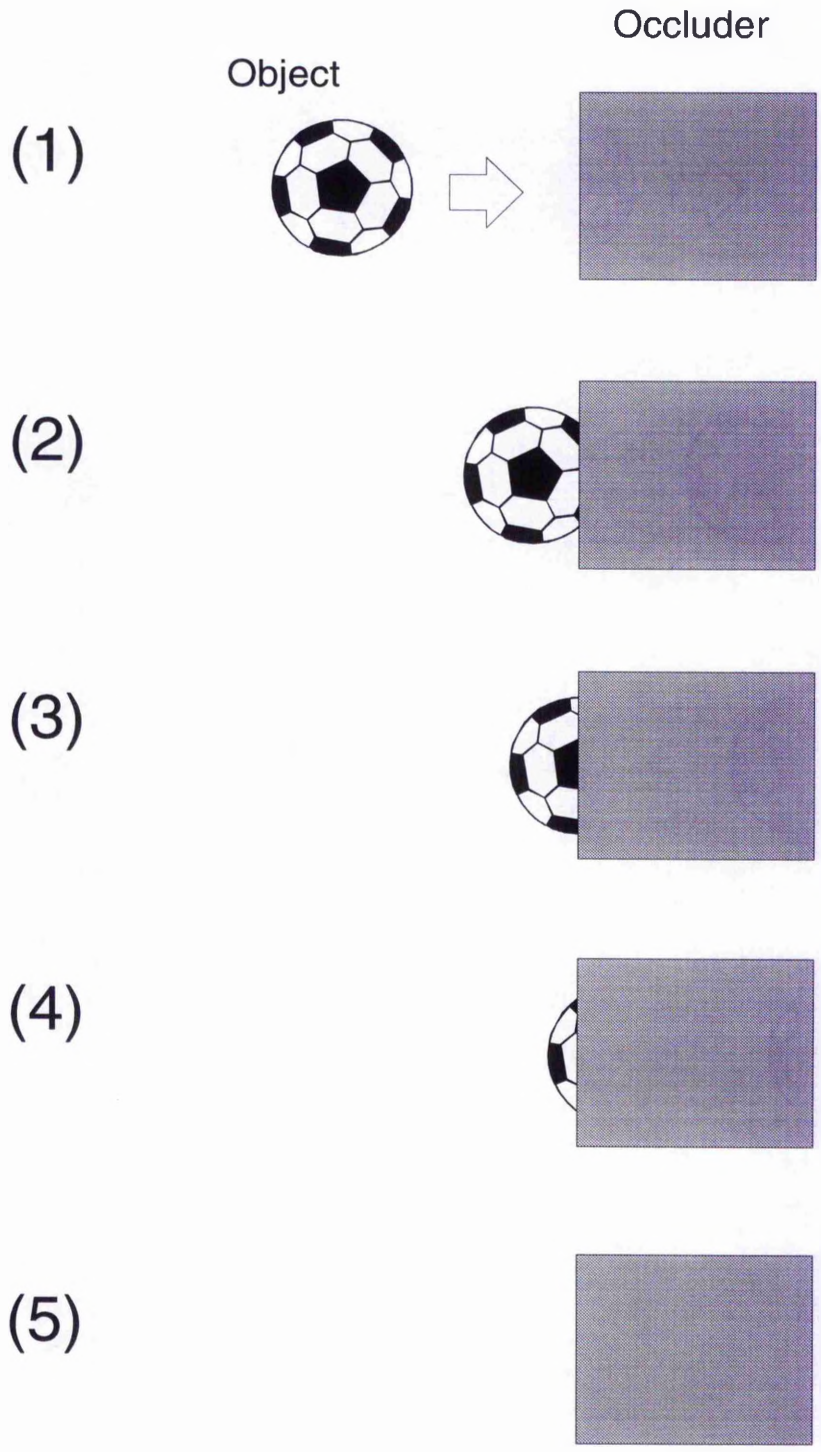


Figure 3.4 Breakdown of the stimulus sequence in gradual occlusion. The object moves towards the occluder (1), and as it moves behind the occluder is gradually and incrementally occluded (2-4) until the object is no longer in view (5).

alternative behavioural measures. For example, Bower (1967) trained 7-week old infants on an operant task in which they sucked in response to the presence of a red and white sphere (conditioned stimulus). The infants were exposed to the red and white sphere under different conditions of disappearance, and it was found that the infants maintained their sucking only under stimulus conditions that signalled the continued existence of the object (e.g. gradual occlusion). If the object disappeared in unnatural ways (e.g. sudden implosion), sucking was discontinued.

The behavioural measure used by Baillargeon and colleagues (Baillargeon *et al.*, 1985; Baillargeon, 1986, 1987) was preferential looking. The assumption underlying this measure is that infants react to novel or surprising events with increased attention. Thus, an infant will look at events that violate its expectations (for example, about object permanence) longer than events that are consistent with its expectations. Baillargeon and colleagues (Baillargeon *et al.*, 1985; Baillargeon, 1986, 1987) habituated infants to the movements of a screen back and forth through a 180° arc (see figure 3.5). After habituation, a box was placed behind the screen and infants were exposed to two test events:

(a) Possible event – the screen rotated and stopped when it reached the box.

(b) Impossible event – the screen rotated 180° as if the box were not there.

They found that 5.5 (Baillargeon *et al.*, 1985), and 4.5 (Baillargeon, 1987) month-old infants looked longer at the impossible than possible test event, suggesting that they were surprised by this outcome and believed the object to still exist after it was occluded. Similar results were obtained for those 3.5 month-old infants that showed rapid habituation during the first phase of the experiment (Baillargeon, 1987).

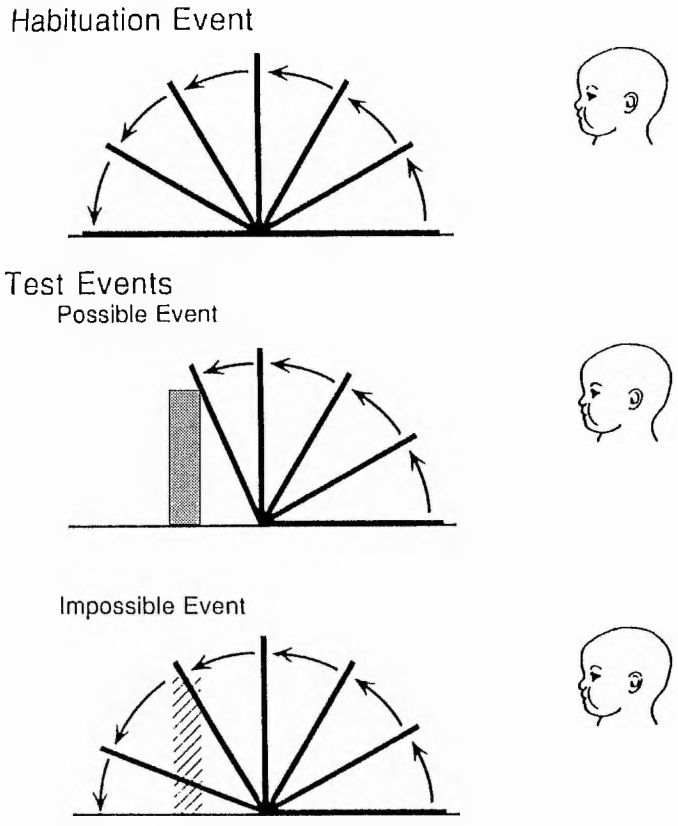


Figure 3.5 Summary of the stimulus conditions used by Baillargeon *et al.* (1985) and Baillargeon (1987). The infants were first habituated to rotation of the screen through 180 degrees. Following habituation, a block was placed behind the screen and the infants were presented with possible and impossible test events. Infants were found to look longer at the impossible than possible event suggesting that they believed the block to still exist after occlusion (from Baillargeon, 1993).

Further experiments using the preferential looking paradigm have shown that 3.5-5.5 month-old infants not only have representations of the existence of objects but also of the properties of objects including height (Baillargeon and Graber, 1987) and position (Baillargeon, 1986).

All this evidence suggests that young infants' knowledge about occluded objects is not entirely different to that of adults. Even before infants' motor capabilities enable them to interact fully with objects, there is evidence for the presence of object permanence. This argues against Piaget's (1954) view of the importance of conceptual ideas about objects, formed through experience, in favour of Michotte (1950). The data should not be taken, however, to imply that object permanence is an innate ability.

3.5 Object permanence in non-humans

3.5.1 Degrees of object permanence

The presence or absence of object permanence and its development has been studied in numerous animal species including cats, dogs, birds and non-human primates (for review see Doré and Dumas, 1987). Piaget's principal tool for observing the development of object permanence was infants' reaction to hidden objects. The same approach has been adopted in the majority of studies in non-humans. Etienne (1973, 1984) has elaborated three different degrees of object permanence that may be observed in animals in the hidden object situation:

(a) stereotyped movements or postures on losing sight of a prey (e.g. invertebrates)

(b) association of visual cues with a particular outcome, but no anticipatory search in a new situation (if A, then B, e.g. chick)

(c) plastic search behaviour relevant to the particular spatial-temporal relationships observed (e.g. dog, chimpanzee)

The first two categories reflect simple behavioural strategies and cannot be considered to represent object permanence. Only with behaviour consistent with the final category can object permanence be said to be present.

In considering object permanence in different species, it is important to be aware of differences in physical characteristics and behaviour. It has been argued that object permanence may be observed in animals only where it is of special selective advantage and this may apply to specific situations (Etienne, 1984).

3.5.2 Development of object permanence

The development of object permanence in different species (e.g. cat: Dumas and Doré, 1989, 1991; dog: Gagnon and Doré, 1994; macaque: Parker, 1977; chimpanzee: Wood *et al.*, 1980, Poti and Spinozzi, 1994; gorilla: Spinozzi and Natale, 1989) seems to follow a similar pattern to that seen in human infants with stages of development similar to those described by Piaget (1954). For example, in a cross-sectional study, Dumas and Doré (1989) found that: 28-day-old kittens would visually track an object moving in their visual field (stage 2); 35-day-old kittens would recover a hidden object but only if they had initiated search before occlusion

(stage 4a); and 48-day-old kittens succeeded on multiple visible displacements (stage 5b). There was no evidence for separate stages corresponding to 4b and 5a. The kittens were not observed to make the A not B error although it is evident in the development of other species, particularly non-human primates (e.g. gorilla: Spinozzi and Natale, 1989; macaque: Poti, 1989)

These patterns of development are evident in both observational (e.g. Dumas and Doré, 1991) and experimental studies (e.g. Gagnon and Doré, 1994). Most experimental studies have used human analogue tests based on the testing of Piaget, the scale devised by Uzgiris and Hunt (1975) for testing human infants, and the Wisconsin General Testing Apparatus.

3.5.3 Level of object permanence

Tables 3.3 and 3.4 summarise the principal studies on the level of object permanence in non-human primates and non-primates, respectively. The stage listed is that claimed by the experimenters as having been achieved. Despite differences in testing procedures, it is clear from these tables that all of the animal species listed reach stage 4 of object permanence - they will search for a hidden object. All non-human primates tested have shown evidence of at least stage 5 of object permanence with the ability to solve visible displacement problems. There is much disagreement, however, over the performance of non-human animals and particularly non-human primates on invisible displacement problems.

Many of these studies have been criticised on methodological grounds (e.g. see Doré and Dumas, 1987; Natale, 1989; Natale and Antinucci, 1989; de Blois, Novak and Bond, 1998). For example, in the Mathieu *et al.* (1976) study, invisible

Cebus monkey	*Cebus apella*	Dumas and Brunet (1994)	5
Cebus monkey	*Cebus apella*	Natale and Antinucci (1989)	5
Cebus monkey	*Cebus apella*	Schino, Spinozzi and Berlinguer (1990)	6
Cebus monkey	*Cebus apella*	Snyder, Birchette and Achenbach (1978)	not clear
Tufted capuchin	*Cebus capucinus*	Mathieu *et al.*(1976)	6
Chimpanzee	*Pan troglodytes*	Mathieu and Bergeron (1981)	6
Chimpanzee	*Pan troglodytes*	Mathieu *et al.*(1976)	6
Chimpanzee	*Pan troglodytes*	Wood *et al.* (1980)	6
Gibbon	*Hylobates lar entelloides*	Snyder, Birchette and Achenbach (1978)	not clear
Gorilla	*Gorilla gorilla gorilla*	Natale *et al.* (1986)	6
Gorilla	*Gorilla gorilla gorilla*	Natale and Antinucci (1989)	6
Crab-eating macaque	*Macaca fascicularis*	Natale and Antinucci (1989)	5
Crab-eating macaque	*Macaca fascicularis*	Schino, Spinozzi and Berlinguer (1990)	5
Japanese macaque	*Macaca fuscata*	Natale *et al.* (1986)	5
Japanese macaque	*Macaca fuscata*	Natale and Antinucci (1989)	5
Rhesus macaque	*Macaca mulatta*	de Blois and Novak (1994)	5
Rhesus macaque	*Macaca mulatta*	Snyder, Birchette and Achenbach (1978)	not clear
Rhesus macaque	*Macaca mulatta*	Wise, Wise and Zimmerman (1974)	6
Stumptail macaque	*Macaca arctoides*	Parker (1977)	6
Orangutan	*Pongo pygmaeus*	de Blois, Novak and Bond (1998)	6
Squirrel monkey	*Saimiri sciureus*	de Blois, Novak and Bond (1998)	5
Squirrel monkey	*Samiri sciurea*	Vaughter, Smotherman and Ordy (1972)	6
Woolly monkey	*Lagothrica flavicauda*	Mathieu *et al.*(1976)	5

Table 3.3 Summary of studies of the level of object permanence in non-human primates.

African Grey parrot	*Psittacus erithacus*	Pepperberg and Funk (1990)	6
African Grey parrot	*Psittacus erithacus*	Pepperberg and Kozak (1986)	6
Cat	*Felis catus*	Doré (1986)	5b
Cat	*Felis catus*	Doré (1990)	5
Cat	*Felis catus*	Doré *et al.* (1996)	5
Cat	*Felis catus*	Dumas (1992)	6a
Cat	*Felis catus*	Dumas and Doré (1989)	5b
Cat	*Felis catus*	Goulet, Doré and Lehotkay (1996)	5
Cat	*Felis catus*	Goulet, Doré and Rousseau (1994)	5
Cat	*Felis catus*	Gruber, Girgus and Banuazizi (1971)	4
Cat	*Felis catus*	Heishman, Conant and Pasnak (1995)	6
Cat	*Felis catus*	Thinus-Blanc, Poucet and Chapuis (1982)	5
Cat	*Felis catus*	Triana and Pasnak (1981)	6
Cockatiel	*Nymphicus hollandicus*	Pepperberg and Funk (1990)	6
Dog	*Canis familiaris*	Doré *et al.* (1996)	6
Dog	*Canis familiaris*	Gagnon and Doré (1992)	6
Dog	*Canis familiaris*	Gagnon and Doré (1993)	6
Dog	*Canis familiaris*	Triana and Pasnak (1981)	6
Illiger mini macaw	*Ara maracana*	Pepperberg and Funk (1990)	6
New Zealand parakeet	*Cyanoramphus auriceps*	Funk (1996)	6
Parakeet	*Melopsittacus undulatus*	Pepperberg and Funk (1990)	6
Ring dove	*Streptopelia risoria*	Dumas and Wilkie (1995)	4b

Table 3.4 Summary of studies of the level of object permanence in non-primate animal species.

displacement consisted merely of hiding the object out of sight of the monkey. This is not at all comparable with the task described by Piaget (1954) and used in many other studies (see section 3.3). In the studies reported by Vaughter *et al.* (1972), Wise *et al.* (1974) and Mathieu *et al.* (1976), subjects received a large number of trials and it is not clear if success results only from the extensive practice. With large numbers of trials, animals may develop simple non-representational strategies that enable them to solve the problem.

Human analogue tests may be unsuitable for different species' behavioural and attentional characteristics (e.g. Dumas and Brunet, 1994). The tests were developed for and validated on human infants, and it is not clear that the same items are valid and relevant for the assessment of cognitive development in non-humans. For example, Gruber *et al.* (1971) reported that cats failed to reach stage 5 of object permanence. In their testing, objects were hidden under pieces of cloth, which the cats had to remove. This is not a particularly easy task for a cat of any age to perform, involving complex motor co-ordination (Doré and Dumas, 1987). In contrast, in tasks in which the occluder is a screen and all the cat has to do is walk round the screen (e.g. Thinus-Blanc *et al.*, 1982; Dumas and Doré, 1989), there is evidence for at least stage 5 of object permanence.

In a longitudinal study of 2 rhesus macaques with three different testing scales, Wise, Wise and Zimmerman (1974) found that the age at which object-related behaviours occurred was test specific. The progression through the different scales was the same, but the rate at which levels of object permanence were achieved varied. This suggests that object permanence is not the only factor affecting performance on the different tasks. Such effects make cross-species comparisons difficult, especially when different tasks have been used for different species.

In cats, failure on invisible displacement problems has been reported in several studies (e.g. Gruber *et al.*, 1972, Doré, 1986, 1990; Goulet *et al.*, 1994). These human-analogue tasks, however, do not represent a natural situation, the tasks are not "ecologically relevant" (Dumas, 1992). An alternative task, designed to mirror natural situations was designed by Dumas (1992). The cats could see a target object through a clear screen, but had to walk round an opaque screen to reach it. During the time that the cats walked round the opaque screen, the object was hidden behind one of two occluders. Thus, the movements of the object occurred out of sight, making the task analogous to the human analogue tests of invisible displacement (see section 3.3). Cats performed successfully on this task suggesting that they are able to represent the concealed movements of objects. In non-human primates, the need for more ecologically relevant tasks has been emphasised by Dumas and Brunet (1994). They argue that in the natural environment invisible displacements involve social objects that are mobile and animate (e.g. conspecifics) and that representational abilities are more likely to be observed in such circumstances.

That a representational strategy is required to solve the human-analogue invisible displacement problems has been questioned (e.g. Schino *et al.*, 1990; Natale and Antinucci, 1989). Such tasks can be solved on a non-representational basis by using a simple searching strategy such as, "search under the last screen touched". Such a rule could be learned by association after a large number of trials and relates to Etienne's (1973, 1984) second degree of object permanence. For example, Natale and Antinucci (1989) tested 3 crab-eating macaques, 2 cebus monkeys and a gorilla on human-analogue invisible displacement tasks designed to disrupt the use of simple search strategies, and examined the pattern of responses and the nature of

errors. They found evidence of representation in the gorilla only, with the macaques and cebus monkeys adopting simple strategies based on task-specific cues.

A recent study by Filion *et al.* (1996) using a different type of task suggests, however, that macaques may be able to represent invisible displacements. The macaques tested had previously been trained to manipulate a joystick to move a cursor around on a computer screen. They were presented with two different tasks. In the first task (HOLE), an object moved around the screen and the monkey had to intercept the object with the cursor. In the centre of the screen was a circular area through which the cursor could not travel. As the object passed through this area it was either visible or invisible (as if the circular area was an occluder). It was found that the monkeys were able to anticipate the position of the object following occlusion suggesting that they were able to represent the unseen trajectory of the object. In the second task (LASER), the monkeys controlled the angle of firing of "shots" from a stationary turret at the bottom of the screen at a target object that moved across the top of the screen. A small rectangular piece of card was placed in front of one portion of the screen to act as an occluder. It was found that the monkeys continued firing during occlusion of the object with angles of firing that suggested inference about movement of the object behind the occluder. Thus it appears that monkeys are able to represent unseen movements. The experimental monkeys had received extensive training in computer tasks, however, and it is not clear what effect this may have had on the monkeys' abilities to infer hidden movement.

In summary, most animal species tested show simple object permanence in that they will search for a hidden object. All non-human primates tested have shown at least stage 5 of object permanence with much disagreement over the capacity to solve invisible displacements. The evidence suggests that there may be a dichotomy

between apes and monkeys with evidence of true representation and ability to solve invisible displacements, similar to that observed in humans, found only in apes (e.g. chimpanzee, gorilla), although the picture is far from clear. More ecologically relevant tasks with socially relevant stimuli, however, may present a different picture.

3.6 SUMMARY

Object permanence is a term that has been used to describe the knowledge that objects have an independent existence and maintain their existence and characteristics even when out of sight. Most non-human species tested show simple object permanence in that they will search for a hidden object. All non-human primates show behaviour consistent with stage 5 of Piaget's object permanence scale. There is conflicting evidence, however, on non-human primates' ability to attain the highest levels of object permanence. Most studies, however, have largely adopted tasks validated on human infants, and behavioural and ecological constraints of different species have often been ignored.

CHAPTER 4

KNOWLEDGE ABOUT OCCLUDED OBJECTS

4.1 Introduction

The literature reviewed in the previous chapter demonstrates that non-human primates possess simple object permanence and are able to follow a sequence of visible displacements. A number of studies have shown, however, that non-human primates cannot follow invisible displacements spontaneously suggesting that they are unable to represent the unseen movements of an object without extensive training. The question remains as to exactly what information non-human primates possess about occluded objects. Do they retain knowledge about the form and nature of occluded objects or simply that there is an object present? It is possible to perform correctly on the basic tests of object permanence simply by remembering that a place is important without having any knowledge of the object that was hidden. Baillargeon (1993; see chapter 3) included two further conditions in her definition of object permanence other than knowledge that the object continues to exist. These specified knowledge that the occluded object retains the spatial and physical properties it possessed prior to occlusion and
that the occluded object is still subject to physical laws. In this section I will briefly review further evidence on the extent of non-human primates' knowledge about occluded objects.

Tinklepaugh (1928, 1932) studied delayed response behaviour in macaques. In the basic version of his task a monkey sat in a chair while a food item (e.g.

banana) was placed under one of two upturned containers. After a delay period the monkey was allowed to leave the chair. Tinklepaugh (1928) found that the monkey would go to the baited container, ignoring the unbaited container, and retrieve the food. Successful performance was not achieved through particular body orientations maintained throughout the delay and the monkeys were able to perform correctly even if removed from the testing room during the delay period. Increasing the length of the delay period did not adversely affect performance and the monkeys were still able to select the correct container after overnight delays of up to 20 hours. These experiments showed that monkeys were able to remember the spatial location at which food had been hidden and similar tasks have been used in testing basic levels of object permanence (see chapter 3). In further, so-called "substitution" experiments, Tinklepaugh (1928) reported evidence for representation of the nature of the reward hidden. The basic procedure of these experiments is summarised in figure 4.1. As in the previous experiments the monkey watched as the experimenter baited one of two upturned containers with a food reward (e.g. banana). During the delay period a screen was raised obscuring the monkey's view of the containers. At the end of the delay period the screen was removed and the monkey allowed to choose one of the containers. In normal trials (top two rows of figure 4.1) the food that the monkey saw hidden was the food retrieved. In substitution trials, however, the nature of the food under the container was changed during the delay period (e.g. from banana to lettuce - bottom row of figure 4.1). Tinklepaugh (1928) describes the typical reaction of one of the monkeys on finding lettuce when the food hidden was banana:

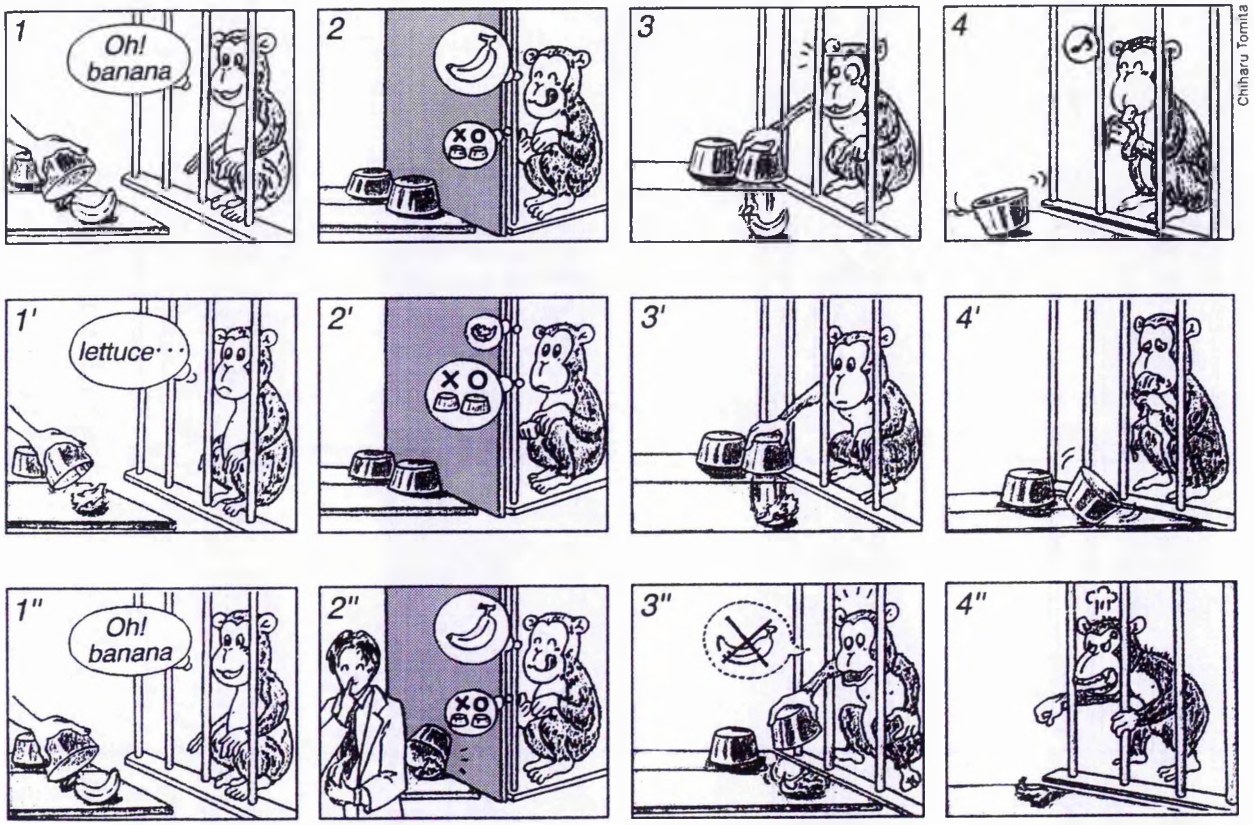


Figure 4.1 The substitution experiments of Tinkelpaugh (1928). In normal trials, banana or lettuce is hidden under one of two upturned containers. During a delay period, the containers are occluded by a screen. When the screen is removed, the monkey can reach out and retrieve the reward. As illustrated in the top two rows of the figure, banana is a higher value reward than lettuce. In substitution trials, the monkey sees one food reward hidden, but during the delay, the experimenter changes the nature of the reward. When lettuce was substituted for banana, Tinkelpaugh (1928) observed prolonged searching and evidence of frustration (from Jennings, 1996)

"She extends her hand to seize the food. But her hand drops to the floor without touching it. She looks at the lettuce, but (unless very hungry) does not touch it. She looks around the cup and behind the board. She stands up and looks under and around her. She picks the cup up and examines it thoroughly inside and out. She has on occasions turned toward observers present in the room and shrieked at them in apparent anger. After several seconds spent searching……the lettuce is left untouched on the floor" (Tinklepaugh, 1928; pp. 224-225)

On normal trials in which lettuce was the food hidden and subsequently found, no such response was observed. The monkey would retrieve and eat the lettuce, giving no signs of anger towards the observers. The observed reaction on the substitution trials was not just a response to the less preferred lettuce as a reward. It is clear that on substitution trials the monkeys had formed expectations about the nature of the reward and were frustrated on finding a different food item. These results, however, do not provide evidence for full representation of the nature of the reward. The results could be explained in terms of the valence of reward. Banana is a high value reward whereas lettuce is a low value reward. When the food is hidden the monkey may be coding only the valence associated with that location.

The characteristic pattern of behaviour described by Tinklepaugh (1928) was observed only on trials in which there was a change from a high value reward to a low value reward. Tests were carried out in which banana was substituted for lettuce (i.e. a change from a low value reward to a high value reward), but there was no discernible behaviour to suggest that the monkeys were aware of the change. Thus the nature of the representation maintained during the delay period is not clear.

In further experiments, Tinklepaugh (1928) found no evidence that the monkeys represented the quantity of food (when a large piece of food was replaced by a smaller piece). When two pieces of food were replaced by one piece, however, there was some evidence for knowledge of the number of items (prolonged searching), but only after the monkeys had received a number of trials on which two pieces of food were hidden. Such a change from two pieces of food to one also represents a decrease in reward in value, analogous to that in the substitution experiments.

There have been few other experiments investigating monkeys' knowledge about occluded objects. The most relevant is the neurophysiological experiment of Watanabe (1996). Recording from neurons in the primate dorsolateral prefrontal cortex, Watanabe (1996) reported neuronal properties consistent with a role in goal-directed behaviour such as that described by Tinklepaugh (1928). Two monkey subjects were trained on delayed response tasks with three reward conditions: (a) visible food; (b) stimulus associated with food; and (c) stimulus associated with liquid. There were two possible response locations and during the cue period, the monkey saw either the food reward itself (visible food condition) or a light stimulus (stimulus associated with food and liquid conditions) at one of the locations. After a delay (5s), the monkey had to respond to the location that had been cued. Half of the neurons tested with different rewards showed differential activity during the delay period relating to the nature of the reward. The majority of these neurons showed greater activity changes during trials with a preferred than a non-preferred reward and the activity was consistent between the different tasks. Watanabe (1996) suggested that the reward-dependent activity was probably related to "retrieving, retaining and/or anticipating the motivational value and visual, gustatory and/or

olfactory images of the specific reward". Each neuron was tested, however, only with a small number of different food and liquid rewards, with different motivational values, and it is not clear if the delay activity represents more than just motivational value of the upcoming reward.

Analogous to the substitution experiments of Tinklepaugh (1928), Watanabe (1996) sometimes changed the nature of the reward in the visible food condition. Such a substitution was observed to "upset the behaviour of the monkey" and trigger prolonged neuronal activation lasting for approximately a minute. In the stimulus associated with food or liquid tasks, the reward obtained was maintained constant over a block of trials. Neuronal activity was monitored during change in reward, from one block to another, over a series of trials. On the first trial following a change in reward, prolonged neuronal activity was observed following presentation of the unexpected reward. Over the following trials the nature of the delay activity changed and activity following delivery of reward diminished. All of these trials involved changes in motivational value (Watanabe, personal communication), and the changes in neuronal response could be reflecting this change rather than more specific qualities of the different rewards.

Two sets of experiments by Hauser (1998; Hauser *et al.*,1996; see also Hauser and Carey, 1998) provide further evidence on the representational capacities of non-human primates. Both sets of experiments rely on the preferential looking paradigm that has been used extensively in studying pre-verbal infants (e.g. Baillargeon *et al.*, 1985; Baillargeon, 1987; see chapter 3). The principle underlying the paradigm is that infants/non-human primates will look longer at events that violate their expectations.

Following methods used by Wynn (1992) in testing human infants, Hauser *et al.* (1996) presented wild rhesus macaques with possible and impossible events in which the number of objects was manipulated (similar to the numeracy experiments of Tinklepaugh, 1928). For example, in one of the possible trials the macaques saw one eggplant lowered behind a screen. After a short delay the screen was removed and one eggplant was revealed. In one of the impossible trials, the macaques saw two eggplants placed behind the screen in succession ('1+1' addition), but when the screen was removed only one eggplant was revealed. Hauser *et al.* (1996) found increased looking times for impossible over possible trials suggesting that the macaques were surprised by outcomes that violated number concepts. These results confirm the observations of Tinklepaugh (1928) in showing that macaques seem to retain a representation of number for occluded objects. The nature of this representation, however, is unclear. Hauser *et al.* (1996) failed to replicate a critical condition of Wynn (1992) in which infants were shown a '1+1' addition and removal of the screen revealed either 2 or 3 objects. Infants showed longer looking times when the result was three than two items, suggesting that the infants are not simply expecting a numerical change but a precise numerical result. An alternative interpretation of the macaque data is that the subjects are not representing individual objects but simply change in the visual display (Hauser *et al.*, 1996). Support for a numeric representation is provided by a recent study (Brannon and Terrace, 1998) showing that macaques represent the numerosities 1 to 9 on an ordinal scale.

In a series of experiments in cotton-top tamarins (a New World monkey), Hauser (1998; see also Hauser and Carey, 1998) presented subjects with a test apparatus consisting of two identical chambers separated by an opaque partition. There was a hole in the partition such that objects could move from one

compartment to the other. An object was placed in one chamber and the apparatus temporarily occluded by a screen. When the screen was removed, the object was either in the same chamber or in the opposite chamber. Objects were classified on three dimensions: (i) self-propelled versus non-self-propelled; (ii) moving versus motionless; (iii) animate versus inanimate. Hauser (1998) found increased looking times for a change of chamber (suggesting concealed movement) for all objects except a live tree frog and mouse (both self-propelled, moving, animate). Even objects that were apparently self-propelled (e.g. small clay face moved by a concealed magnet) elicited surprise if, when revealed, they were in a different chamber to the one they were hidden in. Thus self-propelled motion evident prior to occlusion does not lead to expectations for concealed movement. On the basis of this data, Hauser (1998) proposed that tamarins may be aware of the animate-inanimate distinction. The experiment suggests that tamarins represent the position and the nature of objects (in terms of animate/inanimate) even when out of sight and are able to represent the unseen movements of objects.

The experiment presented here was designed as a quantitative replication of Tinklepaugh (1928) to determine to what extent macaques represent the form and nature of objects that are out of sight. Following Tinklepaugh (1928), food items were hidden behind an occluder which the monkey could retrieve. There was one occluder only since representation of the position of the object was not under investigation. On a small number of change trials the reward hidden was substituted for a different reward of higher, lower or equal motivational value. Behavioural and timing measures were used to analyse the monkey's expectations about the nature of reward.

Following Tinklepaugh (1928), signs of frustration and anger and refusal to eat the reward are expected on change trials where there is a decrease in motivational value. Tinklepaugh (1928) presented only a small number of substitution trials with an increase in motivational value, and frustration or anger (reflecting annoyance at the interference with the food) might also be evident on these trials when assessed more quantitatively. Additionally there may be greater hesitation and increased fumbling of the reward on change trials due to the violation of expectation.

4.2 METHODS

4.2.1 Subject and apparatus

The subject in this experiment was Steve, a male rhesus macaque, who at the time of testing was 4 years old. He was also involved in ongoing neurophysiological studies (see chapters 5-8) and had previously been involved in studies of gaze following (Emery *et al.*, 1997). The apparatus illustrated in figure 4.2 was attached to the front of the primate chair. Throughout the experiment, the monkey was head-restrained in the chair (see chapter 5). The box (370x230x230mm) had walls (painted black) on all sides except for the top which was open. An opening at the front (165x150mm) allowed the monkey to look into the box. On each side, level with the screen was an opening (125x125mm) covered by a flap through which the experimenter could introduce their hand to bait the food well. The food well was shallow so that when baited, the money could see the food reward. The monkey could introduce its hand through an opening in the bottom of the box, which was opened or closed with a sliding trapdoor. Towards the back of the box was a white

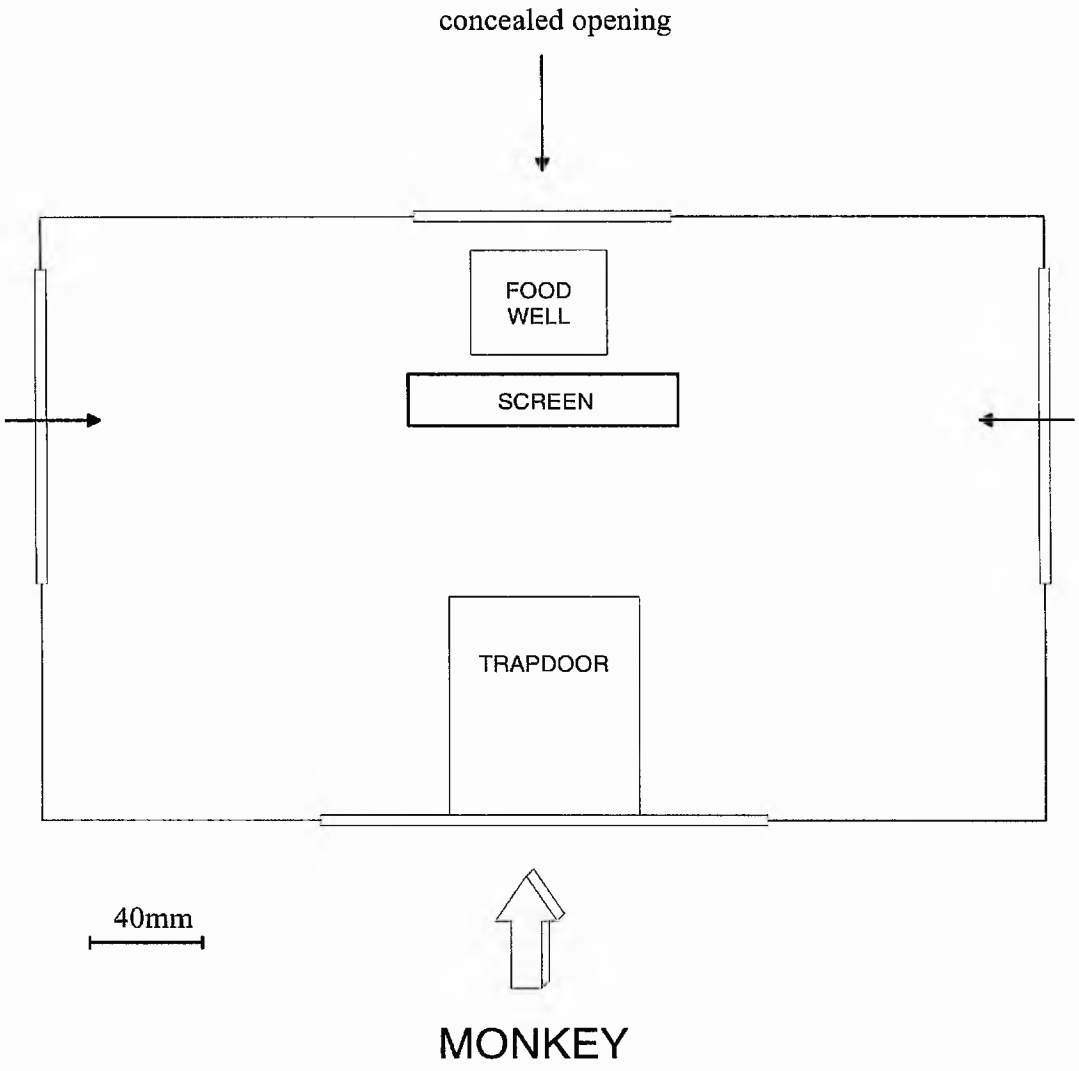


Figure 4.2 Plan view of the reaching box. When the trapdoor was open, the monkey could reach into the box and knock down the screen to retrieve rewards placed in the food well. The experimenter baited the well through one of the side openings, and the concealed opening at the back of the box enabled food rewards to be substituted out of sight of the monkey.

screen (100x120x20mm) which when knocked gently would sink into the floor of the box until the top of the screen was level with the bottom of the box. At the back of the box, out of the monkey's reach, was an infrared camera that was used to record the face of the monkey during trials. Vertically above the box, a second camera recorded all events including the baiting of the well and the reaching movements of the monkey. The images from the two cameras were combined using a Panasonic VHS video mixer (WJAVE7) and a time code was burned onto the combined image with a VITC time code generator and frame counter (Horita VG50).

A variety of different rewards were used including strawberry, carrot, cabbage, banana and maltesers (chocolate). All pieces of food were cut up to be approximately the same size. Food rewards that were given to the monkey freely in the home cage were classed as low value rewards (apple, carrot, and cabbage). All other rewards were classed as high value (e.g. peach, grape, banana). In addition on some trials, the monkey was shown the experimenter's empty hand and the well was not baited. These were also classed as low value trials.

4.2.2 Training

The subject was first trained to reach out from the primate chair, take food from the experimenter and feed himself. Very little training was required and the reaching box was quickly introduced. Initially the trap door was held open and the screen was always lowered. After a short period of familiarisation the monkey put his hand up into the box to search the surroundings. Food was initially held close to the open trapdoor for the monkey to reach and in a series of trials the distance of the food from the opening was gradually increased. The experimenter's hands always

entered into the box through the side openings and never through the open top of the box or the concealed opening. Once the monkey was happy reaching into the box to take food, the screen was raised and lowered. Initially the monkey reacted adversely to movement of the screen, but after a few trials became unconcerned. In a series of trials the screen was held in the raised position and food held close to its front surface. The food was moved closer to the screen until eventually it was placed above the screen and finally just behind the screen. On some of these trials the monkey knocked the screen and it dropped into the floor of the box. Initially there was an adverse reaction, but again after a few trials the monkey habituated to movement of the screen when it knocked it. The food was held lower and lower behind the screen and the monkey was now forced to knock down the screen to reach the food. In all of these trials the experimenter's arm remained in view and served as a cue for the presence of reward behind the screen. The monkey reached into the box very soon after the experimenter's arm entered the box. At this stage the trapdoor was brought into use. The trapdoor now remained closed until the well had been baited and the experimenter had removed his arm from the box.

4.2.3 Experimental procedure

At the start of a trial the trapdoor was closed and the screen was lowered. The experimenter put one arm through one of the side openings of the box and showed an item of food to the monkey to attract its attention. Once the monkey was looking at the food, the item was placed in the food well and the screen raised. The experimenter reached into the box through the concealed back opening, removed the reward and either returned the reward back to the well or replaced it with a different

reward. On change trials, the food was changed to another food reward, similar in size, of equal, higher or lower motivational value. On all trials the experimenter reached into the box through the concealed opening and removed the food. Thus there were no sound cues or changes in light uniquely associated with trials in which the food reward was changed. The trapdoor was opened and the monkey allowed to reach into the box. If the monkey did not reach within 10 seconds the trapdoor was closed. If the monkey reached into the box, the trial ended when the monkey withdrew its hand completely, usually after first eating the food reward. In a given session, trials were run until the monkey made at least 3 consecutive non-reaches for high value rewards and gave no evidence of wanting reward when presented freely or had completed at least 80 trials.

The frequency of change to no-change trials was approximately 1:10 with consecutive change trials separated by at least 3 no-change trials.

4.2.4 Analysis

Video recordings made of the test sessions were analysed for timings of the different phases of the monkey's performance and the occurrence of specific behaviours recorded quantitatively.

(a) Behavioural measures

(A) Timing

(i) REACTION: Time from opening of the trapdoor to touching the screen – this is a measure of the speed of reaction of the subject and includes the

time to initiate reach and the duration of the reach. Faster reaction times may reflect greater motivational values of rewards.

(ii) RETRIEVAL: Time from touching the screen to withdrawing hand beyond the edge of the trapdoor – this is a measure of the time taken to pick up the reward, and will be increased by any hesitation or fumbling.

(iii) WITHDRAWAL: Time from withdrawing the hand beyond the trap door to the food touching the mouth – this is a measure of the speed of bringing the food back to the mouth and includes any time during which the food might be examined visually before being consumed.

(B) Events

(i) PREPARATORY MOVEMENTS – movements of the hands prior to the opening of the trapdoor after the screen has been raised. Such movements involved pushing at the trapdoor and were taken to indicate an impatience to reach, consistent with high motivation.

(ii) REACH – whether the monkey reached for the food or not. Lack of reaching may indicate lack of motivation.

(iii) PICK-UP – on trials in which the well was baited and the monkey reached, whether the food was picked up cleanly or the monkey fumbled. A pick-up was determined to be "clean" if the monkey grasped the food and immediately lifted it into the air. Any fumbling or dragging of the reward was deemed not to be a clean pick-up.

(iv) EAT – on trials when the monkey made a reach, whether he actually ate the food. Failure to eat the food may reflect violation of expectation.

(v) CHAIR SHAKING - after knocking down the screen whether the monkey exhibited any signs of frustration by shaking the primate chair. Any shaking of the chair up to the beginning of the next trial was counted.

In addition eye position and eye movements were noted throughout all trials.

(b) Statistical analysis

Timing measures were analysed using non-parametric Mann-Whitney U-tests. Frequencies of specific events were examined using chi-squared analysis with the Yates correction for 2x2 contingency tables. In cases where there was a small number of trials with expected frequencies less than 5, the Fisher exact test was used. For all tests, the level of significance was taken as $p<0.05$. All trials were analysed in comparisons of preparatory movements and reaches regardless of whether the trial was a change trial or not. For analyses of the frequency of clean pick-ups and eating and the retrieval timing measure only those trials in which there was a reach and a reward to be picked up were included. Analysis of shaking included all trials in which there was a reach. Except for investigating preparatory movements and reaching, analyses of high and low value trials excluded all change trials.

4.3 RESULTS

After approximately two months of training, testing was initiated. Steve completed 5 sessions over a period of three weeks, comprising a total of 399 separate trials. Out of this total, 35 trials (8.8%) involved a change in reward. In terms of motivational value, these change trials consisted of 13 with no overall change in reward value (9 high-high, 4 low-low), 18 with a reduction in the motivational value

of the reward (8 high-low, 6 high-nothing, 4 low-nothing), and 4 with an increase in the motivational value of reward (all low-high). A complete summary of the trials, responses and timings is given in appendix A. Consecutive trials occurring at the end of a session on which Steve didn't reach were assumed to represent satiation and were excluded from the analysis.

The results are summarised in tables 4.1 and 4.2 with the trials broken down separately into change and no-change trials, and high and low value reward trials, respectively.

There was a characteristic pattern of eye movements on every trial. At the start of a trial, the eyes were directed at the trapdoor. As soon as the trapdoor started to open, the eyes moved up in the direction of the screen. The eyes followed the hand as the screen was knocked down and remained directed at the hand as the food was brought back to the mouth. No differences were observed in the pattern of eye movements between change and no-change trials or between high and low value reward trials.

Analysis of preparatory movements (regardless of whether the food was changed on that trial) shows a significantly higher proportion on high value reward trials than on low value reward trials. Preparatory movements are taken to imply an impatience to reach, suggesting that prior to reaching, the monkey was aware of the value of the reward that had been hidden. There is no significant difference between the proportion of preparatory movements on change versus no change trials, suggesting that the monkey was unaware of the manipulation taking place on change trials.

There is also a significant difference between high and low value reward trials in the proportion of trials that the monkey reached for the reward. The monkey

		Change	No change	U	χ^2	p
Timings:	Reaction	22.0 (34)	21.1 (293)	4432.5		p>0.05
average time	Pick-up	48.0 (24)	31.2 (287)	1982.0		p<0.001
(frames)	To-mouth	18.9 (19)	15.9 (284)	2361.5		p>0.05
Events:	Preparatory movements	24 (35)	208 (350)		0.76	p>0.05
number of	Reach	35(35)	299(350)			
occurrences	Clean pick-up	10 (25)	184 (295)		3.94	p<0.05
	Eat	19 (25)	284 (295)		15.01	p<0.0005
	Shaking	10 (35)	35 (350)		8.91	p<0.005

Table 4.1 Comparison of change and no-change trials. The number of trials for each condition is shown in brackets.Timing measures were compared using the Mann-Whitney U-test, whereas event measures were analysed using chi-squared.

		High	Low	U	χ^2	p
Timings: average time (frames)	Reaction	20.7 (247)	23.2 (46)	6806.5		p>0.05
	Pick-up	31.7 (245)	27.2 (43)	4424.5		p>0.05
	To-mouth	16.4 (248)	12.6 (36)	3961.0		p>0.05
Events: number of occurrences	Preparatory movements	200 (310)	32 (75)		11.14	p<0.001
	Reach	275 (310)	59 (75)		4.46	p<0.05
	Clean pick-up	152(252)	32(43)		2.54	p>0.05
	Eat	248(252)	36(43)		18.18	p<0.0001
	Shaking	24(287)	11(63)		3.79	p>0.05

Table 4.2 Comparison of high- and low-value reward trials. Conventions are the same as table 4.1.

was more likely to reach for the reward if it was of high motivational value than low motivational value. The proportion of reaches between change and no change trials cannot be analysed since a change trial was counted as such only if the monkey reached for the reward i.e. only if the monkey discovered the change.

On the timing measures there are no significant differences between the high and low value reward trials. Thus, although the monkey made a greater proportion of preparatory movements and reaches on high than low value reward trials, when he did reach he reached and picked up the reward with the same degree of hesitation and at the same speed. He was not faster to pick up and eat a high value reward compared with a low value reward.

Similarly, comparison of change versus no change trials shows no significant difference for the reaction and withdrawal timing measures. There is, however, a significant difference between the time taken to retrieve the reward on change and no-change trials with more time taken on change trials. This could result from the monkey hesitating once the reward object became visible and the change apparent, from difficulties in picking up the unexpected reward, the monkey searching for the reward that he saw hidden or from a combination of these factors. Comparison of the trials on which there was a change in the motivational value of the reward (high-low, low-high) with trials in which there was no change in motivational value (high-high, low-low) shows no difference in the retrieval time ($U=62.0$, $p>0.05$). Dividing the change trials into those in which there is a decrease in motivational value (high-low) and those in which there is no decrease (high-high, low-low, low-high) also reveals no significant difference ($U=51.5$, $p>0.05$). Therefore, it is change in reward that is important and not change in valence or decrease in valence.

Comparisons of change versus no-change trials shows significant differences in the proportions of clean pick-ups, food eaten and shaking.

There is a significantly higher proportion of clean pick-ups on no-change than change trials, suggesting that the monkey had greater difficulty in picking up the reward when it was unexpected than expected. This could account for the timing difference observed in the retrieval period.

Analysis of the proportion of clean pick-ups for different rewards (presented on at least 8 separate trials), also shows a significant difference between the different rewards (χ^2=42.34, $p<0.01$ – see appendix A). This difference, however, was due to the difficulty in picking up smarties (oval-shaped sweets - high-value reward) and exclusion of smartie trials from the analysis reveals no significant differences amongst the remaining rewards (χ^2=23.9, $p>0.05$). This difficulty in picking up smarties cannot account for the observed difference between change and no-change trials since a smaller proportion of smarties was presented on change trials than no-change trials.

On trials in which the monkey reached, there was a higher proportion of failures to eat the food on change trials than no-change trials. There was also, however, a significant difference between high and low value reward trials with more failures to eat the food on low than high value trials. Comparison of change trials in which the reward was changed to a low value reward (high-low and low-low) with no-change trials in which a low value reward was hidden and the same reward was retrieved shows a significant difference in the number of failures to eat the food (change to low: 6/12; no change, low: 7/43; Fisher exact test, one tailed, $p<0.05$). The monkey was much more likely not to eat the reward when it was changed to a low-value reward than when there was no change and a low value

reward was retrieved. On change trials, all failures to eat the reward occurred on high-low value change trials. A comparison of high-low and low-low value change trials shows a significant difference in the proportion of non-eating trials (high-low: 6/6; low-low: 2/6; Fisher exact test, one tailed, $p<0.05$).

Comparison of the change and no-change trials shows a significantly greater proportion of shaking on change trials than no-change trials. There is no significant difference in shaking between high and low value trials. Eight out of ten of the change trials on which shaking occurred were trials with a decrease in reward value (either high-low, or low-nothing). Comparison of the change trials on which there was a decrease in reward value (high-low, high-nothing, low-nothing) with those in which there was no decrease (high-high, low-low, low-high) shows a significantly higher proportion of shaking on those trials with a decrease in the value of the reward (decrease: 8/18; no decrease: 2/17; Fisher exact test, one tailed, $p<0.05$). Dividing the change trials into those with a change in reward value (high-low, high-nothing, low-nothing, low-high) and those with no change in reward value (high-high, low-low) shows no such difference in the proportion of trials on which shaking occurred (change value: 8/22; no change in value: 2/13; Fisher exact test, $p>0.05$).

4.4 Discussion

This experiment shows quantitatively that monkeys appreciate the motivational value of objects out of sight, and provides some evidence to suggest that they also maintain a representation of the form of objects. The monkey tested showed a greater proportion of both preparatory movements and reaches on high value than low value trials. On trials in which the nature of the food was changed,

the monkey showed an increased time to pick up the reward, a smaller proportion of clean pick-ups, a greater proportion of shaking and an increased likelihood of not eating the food than on no-change trials.

4.4.1 Evidence for representation of motivational value

Steve showed a greater proportion of preparatory movements and actual reaches on trials in which he saw a high value food reward hidden behind the screen than a low value reward. Preparatory movements consisted of pushing up against the closed trapdoor and are taken to imply an impatience to reach. Subsequent reaching suggests that the monkey wanted the reward. Both these measures suggest that prior to pushing down the screen the monkey is aware of the motivational value of the reward that was hidden. Preparatory movements could be initiated whilst the reward was still in sight and may help the monkey to maintain a representation of high motivational value.

Frustration, anger and refusal to eat the reward were reported by Tinklepaugh (1928) to occur on substitution trials in which there was a decrease in the motivational value of the reward. In the current study, the monkey was less likely to eat the food reward on change than no-change trials. This difference was largely due to the monkey's refusal to eat the reward on change trials in which there was a decrease in the value of the reward (high-low). Similarly the monkey was more likely to shake the primate chair (a sign of frustration or anger) on change than no-change trials. Again this difference was largely due to shaking on change trials in which there was a decrease in the motivational value of the reward (high-low, high-nothing, low-nothing). These results show that decreases in the motivational value of

the reward lead to frustration or anger and a refusal to eat the reward and imply that the monkey maintains a representation of the motivational value of the reward during occlusion.

In themselves these results do not necessarily imply a representation of the actual identity of the food reward. One limitation of Tinklepaugh's (1928) research is that his qualitative descriptions can be interpreted as evidence for motivational value alone.

4.4.2 Evidence for representation of object form

The monkey showed an increased retrieval time and a lesser proportion of clean pick-ups on change than no-change trials. The difference in the proportion of clean pick-ups may largely account for the differences in retrieval time. The differences were not due to selective increases on trials in which there was a decrease in motivational value, or trials in which there was simply a change in motivational value. These results suggest that the monkey was less efficient at picking up and retrieving the reward when the identity of the reward was unexpected even if reward value was equivalent. Although the pieces of food were all of roughly equal size they differed in shape and firmness and the monkey was observed to use slightly different strategies in picking up different food rewards. Changing the nature of the reward may affect the effectiveness of any pre-planned motor strategies. These results suggest that the monkey maintained a representation of the form of the object during occlusion.

4.5 Summary

Although there is much evidence showing that macaques and other non-human primates exhibit simple object permanence, the nature of any representations about those objects is unclear. In the experiment described here, a macaque subject retrieved occluded food rewards that could be changed out-of-sight of the monkey. The qualitative results of Tinklepaugh (1928) were replicated and extended quantitatively, showing that macaques are aware of the motivational value of occluded food rewards. Furthermore the increased time and more frequent errors in picking up a reward on change trials compared with no-change trials suggests that macaques maintain some sort of representation of the form of the occluded object.

CHAPTER 5

GENERAL EXPERIMENTAL METHODS

5.1 SUBJECTS

The subjects used in the neurophysiological experiments were two male juvenile Rhesus macaque monkeys (*Macaca mulatta*): Steve, 4 years, 10-12kg and Terry, 3 years, 4-6kg. Throughout the training and recording period the monkeys were housed individually, separate from their colony but in auditory and visual contact with the other monkeys.

All procedures conformed to UK Home Office guidelines for animal experimentation and were performed under appropriate Home Office project and personal licences.

5.2 TRAINING AND BEHAVIOURAL TASK

5.2.1 Basic training

Once training was initiated, the subjects' food and water access was restricted. Food in the home cage was limited to dry pellets, some vegetables, and apples. During weekdays, water intake was restricted overnight and was available during training and *ad libitum* for a restricted period after each daily training session. At weekends, water was available *ad libitum.*

The monkeys were initially familiarised with the experimenter and the room in which electrophysiological recordings were to take place. They were taken out from their home cages in a small travel cage, transported to the recording room and given food and water over a period of 30 minutes. Once the monkeys were comfortable with being taken out (usually after 2-3 days) and were freely taking food and water from the experimenter, the primate chair was introduced. The subjects were trained to climb into the primate chair and to be comfortable with their head upright and restrained by a neck plate. The amount of time the monkeys were kept out of their cage was slowly increased until they were happy remaining in the recording room for up to 4 hours, showing no signs of discomfort or anxiety.

During this period food and water was no longer given freely and the subjects were trained on a visual colour discrimination task which was employed during recording to ensure fixation on the screen on which slide and video stimuli were presented.

5.2.2 Visual colour discrimination task

Initially, the subjects were trained to accept fruit juice from a syringe. This was offered freely by the experimenter. A pair of metal lick-tubes was introduced, connected to the front of the primate chair and the monkey was encouraged to lick at these to gain the fruit juice reward. The lick-tubes were connected to a two-syringe, two-valve pipetter (Microlab 940, Hamilton, UK) which dispensed liquid whenever the circuit between the tubes and the chair was closed i.e. whenever the monkey placed its tongue in contact with the tubes. Once the monkey was licking freely at the tubes, training was initiated on the colour discrimination task. Through the lick

tubes the monkey could either be given fruit juice or a mildly aversive, dilute saline solution. Throughout training, reward was always paired with an LED illuminated green (directly in front of the monkey) and saline was paired with the LED illuminated red. Before illumination of the LED (either red or green), there was a 0.5 second tone. The LED remained illuminated as long as the appropriate solution was being delivered. At the start of training, reward was available for 5 seconds.

Once the discrimination had been learned the distance of the LED from the monkey was increased until the monkey was attending to an LED illuminated on a white screen at a distance of 4.4m on which stimuli could be displayed. The length of time that the LED was illuminated at one particular colour, and hence the reward duration, was slowly decreased to maximise the number of trials that would be performed during recording. The minimum duration used was 1 second. The percentage of trials that reward was available compared to aversive solution was also slowly reduced until a ratio of 1:1 was achieved.

5.3 Surgical procedures

5.3.1 Implant

Once the subjects had been trained successfully on the task and were beginning to perform the visual colour discrimination, they were prepared for surgical implant of recording wells to allow electrodes to be introduced into the brain. Several days before the operation, a stereotaxic implant frame (see figure 5.1) was made containing two stainless steel David Kopf recording wells (16 mm internal diameter) and two plastic tubes (5mm internal diameter). When the monkey was in

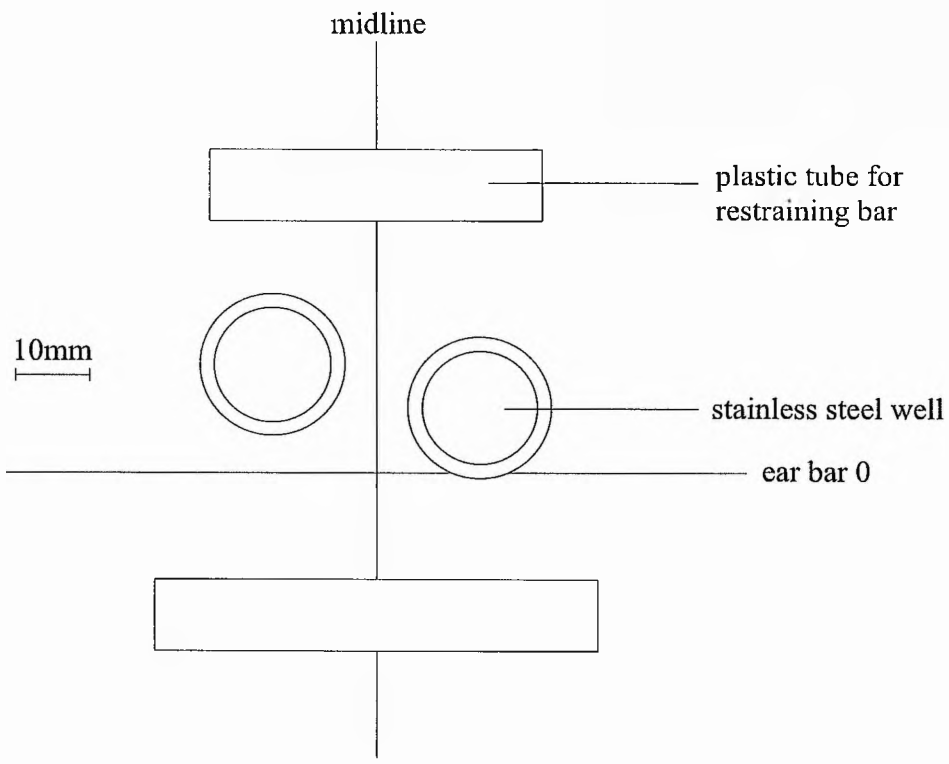


Figure 5.1 Scale plan of the implant frame for Terry showing the positions of the wells and the plastic tubes for the restraining bars.

the primate chair, metal rods could be passed through the tubes and clamped to the primate chair to secure the monkey's head. The target area was the upper bank of the anterior superior temporal sulcus (areas TPO and PGa of Seltzer and Pandya, 1978). On the basis of previous sites for the positioning of the wells, the stereotaxic co-ordinates in mm (relative to ear bar 0) for the centres of the wells were: Terry - 9 anterior, 14 lateral (right hemisphere) and 15 anterior, 14 lateral (left hemisphere); Steve – 11 anterior, 14 lateral (right hemisphere) and 15 anterior, 14 lateral (left hemisphere). Once these co-ordinates had been determined a diagram of the implant was made accurately on graph paper and placed under a sheet of glass. The two plastic tubes were located perpendicularly to the mid-line of the implant so that the distance between the centres of the tubes was approximately 65mm. The components of the implant were placed over the corresponding part of the diagram and connected together with dental acrylate (Autenal Dental Products Ltd., Harrow, England). Small quantities of the acrylate were dripped carefully around the implant components forming a thin web linking them together. After the dental acrylate had hardened a small amount of water was placed around the edges of the frame and it was loosened from the glass. The frame was attached to the stereotaxic apparatus so that it could be lowered onto the skull of the monkey during the surgical procedures.

5.3.2 Surgery

Twenty-four hours before the operation the monkey's access to food was restricted, and twelve hours before it, access to water was restricted. Pre-operatively the monkey was given a weight-dependent dose of ketamine (to sedate it), 1ml amfipen (100mg/ml ampicillin - a wide-acting antibiotic) and 1ml of 600μg/ml

atropine (to reduce the production of saliva during the operation). A few drops of liquid paraffin were placed in the eyes to prevent them drying up. The head of the monkey was shaved and swabbed with alcohol and an intravenous cannula was placed within the saphenous vein. Full sterile procedures were observed during the operation.

The monkey was positioned in a stereotaxic apparatus, its head held firmly in place by ear bars and orbital ridge grips. The intravenous cannula was connected to a three-way tap so that both saline and barbiturate (Sagatal - to anaesthetize the monkey) could be administered. The monkey's body temperature was monitored throughout the operation and regulated with an electric blanket and a fleece cover that could wrapped around the body. Breathing rate was also noted at regular intervals. Once Sagatal had been administered to the monkey the depth of anaesthesia was monitored by checking for stretch reflexes, and more barbiturate was administered as necessary.

An incision was made in the scalp roughly at the midline from just above the eye-ridges to the back of the crown of the head. The skin was reflected, held back in place with haemostats and the exposed skull cleaned. Any localised bleeding was cauterised. The implant frame attached to the stereotaxic apparatus was lowered onto the surface of the skull and the edges of the recording wells marked with a chinagraph pencil. The implant was raised from the skull and a craniotomy performed. The marked areas were drilled out under constant irrigation with water (to prevent the bone becoming too hot), drilling vertically rather than perpendicular to the skull surface, and leaving the dura intact. The implant was again lowered onto the skull and several self tapping screws and H-shaped pieces of stainless steel inserted through holes drilled into the skull, to enable the implant to be secured

firmly. Liquid dental acrylate was applied carefully around the implant, screws and H-pieces, making sure that none obscured the bottom of the recording wells. The acrylate was built up so that all components of the implant frame were fully secured.

Post-operatively, the monkey was returned to the home cage and within two hours had regained consciousness and was mobile.

The dura inside the recording wells was regularly cleaned and swabbed out with saline and an anti-bacterial agent (PEP, 3% powder, Intervet Laboratories Ltd., England) applied as necessary. When not in use the well caps were covered with plastic caps. The monkey was given two to four weeks to recover from the operation before training was resumed, as preoperatively, but with the addition of head restraint. Two metal restraining bars were placed through the plastic tubes of the implant and clamped to the sides of the primate chair.

5.4 Electrophysiological recording methods

Electrophysiological recordings were initiated once the monkey had achieved sufficient proficiency in the tasks on which it had been trained (performing at least 70% correct trials). The monkey's head was restrained in the primate chair and a topical anaesthetic, lignocaine hydrochloride (Xylocaine 40mg/ml) applied to the dura within the recording well to be used. After five minutes (allowing time for the anaesthetic to act) a David Kopf micro-positioner (adjusted to predetermined stereotaxic co-ordinates) was fixed to the recording well and a trans-dural guide tube (outer diameter 1.0mm) inserted through the dura and into the surface of the brain. A tungsten glass microelectrode (outer diameter 0.5mm, after Merrill and Ainsworth, 1972) was pushed through the guide tube until its tip was 20mm below the dura. The

electrode was further advanced with a hydraulic microdrive (David Kopf 607W) or a manual Wells hydraulic microdrive and the depth of the electrode at any given point recorded.

Single cell activity was amplified (Neurolog NL104), filtered with a 50Hz notch filter together with high pass (800Hz) and low pass (20kHz) filters (Neurolog NL125), and monitored with two oscilloscopes and an audiomonitor. One of the oscilloscopes operated through a time delay so those elements of the response rising above a threshold value could be examined further. The signals were converted to TTL pulses by a spike processor (Modified Digitimer DM130) and sampled with an AT compatible personal computer (Dell 386) and digital interface unit (Cambridge Electronic Design 1401). Additionally the filtered signal was recorded on a VHS video recorder.

At the end of every recording session the position of the electrode was determined by taking frontal and lateral x-radiographs of the monkey's head with the electrode still in position.

5.5 General testing procedures

The electrode was advanced through the brain until cellular responses were encountered. Isolated cells were tested clinically by presenting a wide range of visual, auditory and somatosensory stimuli to the monkey as it sat in the primate chair. Visual stimuli presented included junk objects, food items and the experimenter in a wide range of postures and movements. Auditory stimuli included vocal sounds, electronic noises and any sounds that could be produced with the junk objects available in the room. The front of the primate chair could be opened and it

was possible to present somatosensory stimuli over the entire body surface of the subjects. Cells showing changes in activity in relation to any of these stimuli were tested further. Cell responses could be tested in more detail using a 20cm square liquid crystal shutter (Screen Print Technology Ltd., rise time <15ms) placed 15cm in front of the monkey's eyes and fully enclosed. Under the control of the computer, the shutter became transparent for a specified duration (usually 1s) following a 0.5 second tone. During the opening of the shutter, stimuli could be presented in isolation. Cells could be tested both with 3-D stimuli and with 2-D stimuli projected onto a screen. During the opening of the shutter the central LED was illuminated on the screen (either red or green) to ensure attention to the stimuli. Stimuli were also replayed from a laser video disc (RLV Mk II, Optical Disc Corp.) with a video disc player (Philips VP406 Laser Vision Disc Drive) and projected onto the screen using a colour video projector (Sony VPH-1041QM) under computer control. VHS and S-VHS videotapes could also be displayed as stimuli through the projector.

During testing, stimuli were presented in a pseudo-random order either from pre-planned protocols, or protocols constructed during testing. At regular intervals, the monkeys were fed small pieces of fruits and vegetables to maintain alertness.

An infrared camera inside the shutter box enabled the monkey's eye movements to be monitored during testing.

5.6 Reconstruction of the electrode tracks

5.6.1 Overview

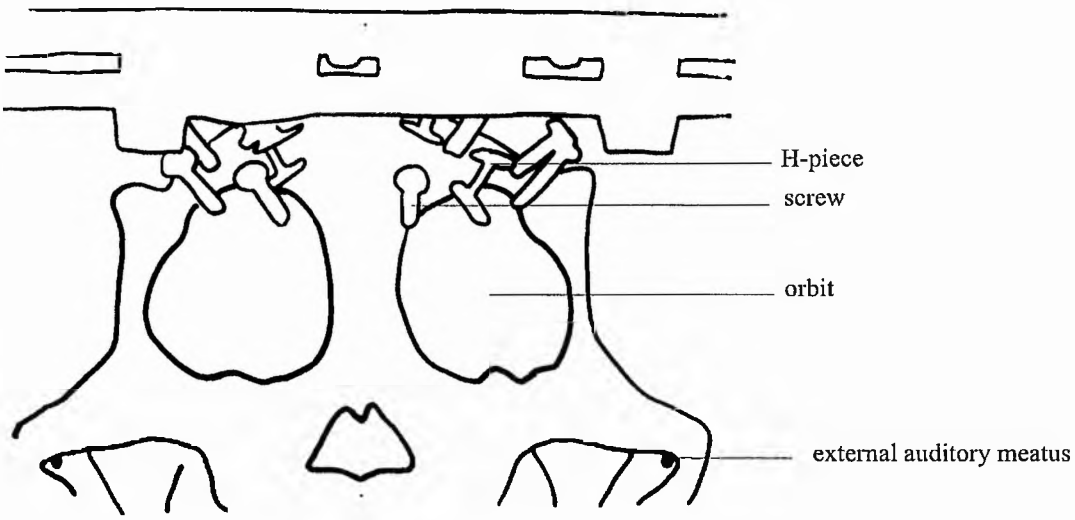
The cells recorded can be localised using x-ray, MRI and histological evidence. The brain "maps" created by each technique can be aligned using markers visible in two or more of the techniques. The microelectrodes used for recording are visble on both x-rays and MRI, and fluorescent dye coating the final electrode and a micro-lesion placed at the end of the final recording track enable the x-rays and MRI to be aligned with histological sections. X-rays provide localisation relative to the skull, whereas MRI and histology enable the tracks to be localised with respect to the sulci and other brain structures.

5.6.2 X-ray reconstruction

The lateral and frontal X-rays taken at the end of every recording session show the position of the electrode relative to bony landmarks and the screws used to secure the implant. Figure 5.2 shows examples of tracings from X-rays (of Steve) with the prominent landmarks labelled. The posterior clinoid process and the sphenoid bone have been reported to be good predictors of the height and anterior position of the amygdala (Aggleton and Passingham, 1981) and provide a useful landmark in localising the current neurophysiological recording tracks.

For reconstruction of the electrode tracks, the trajectory and position of the electrode tip were calculated from each X-ray relative to a co-ordinate system superimposed on the visible landmarks (see figure 5.3). For the frontal X-ray, a

Frontal



Lateral

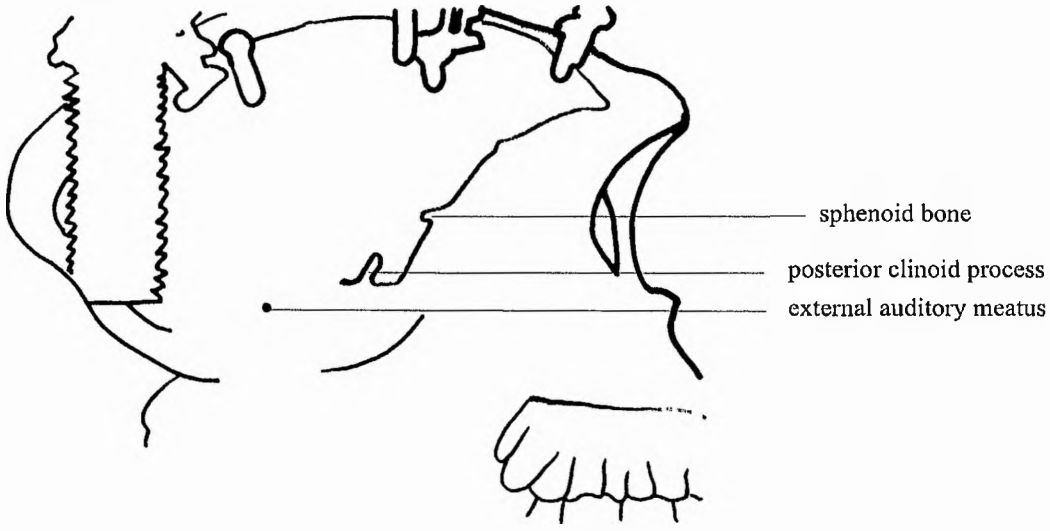


Figure 5.2 Tracings from examples of frontal and lateral x-rays of the monkey subject, Steve, with the principal "landmarks" labelled (not full size).

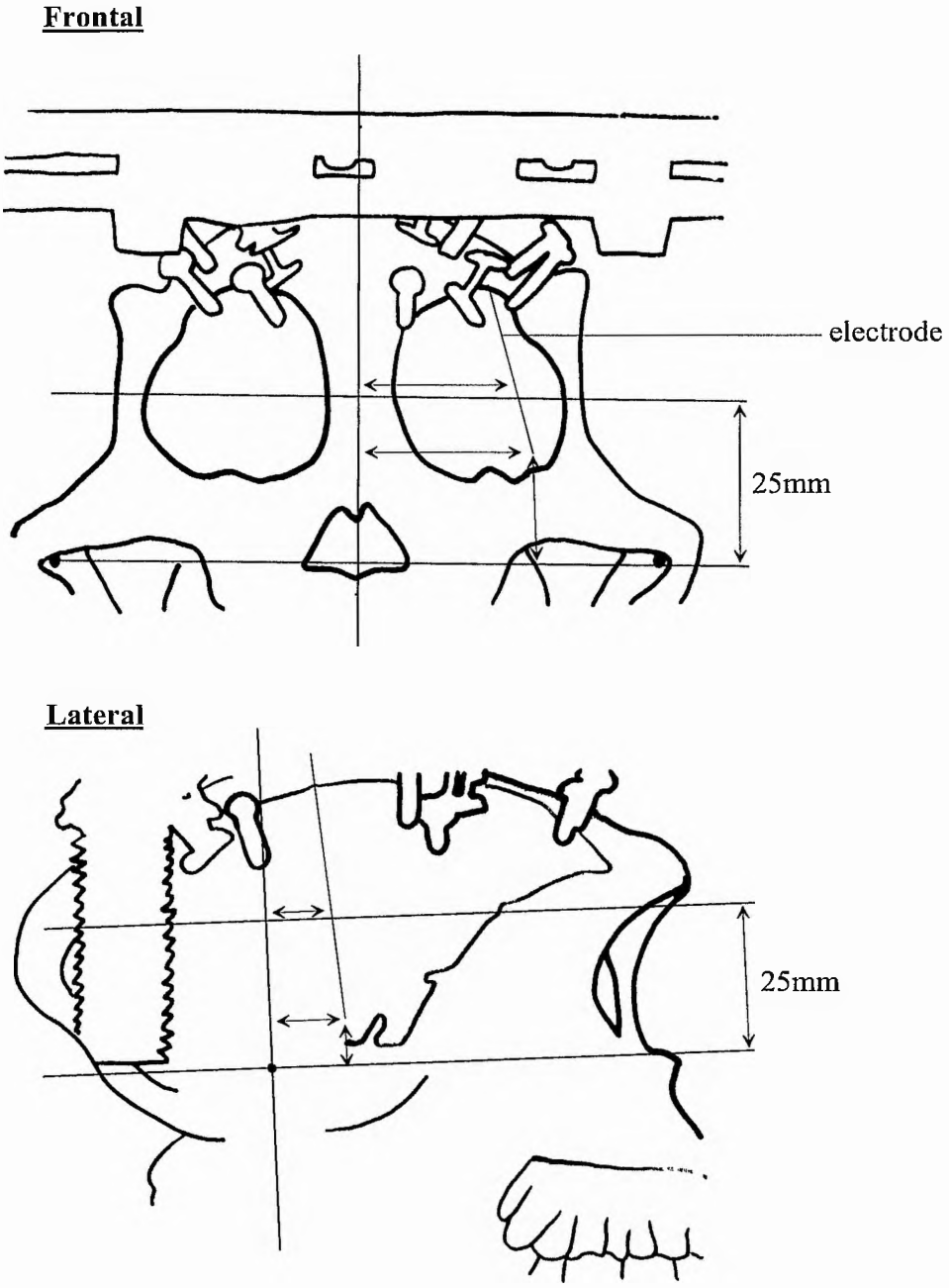


Figure 5.3 Tracings from frontal and lateral x-rays of the monkey subject, Steve, showing the measurements used for reconstructing the electrode tracks (not to scale).

horizontal axis was drawn between the two auditory canals, and a second, vertical axis perpendicular to the first at the mid-point of the skull. The distance of the electrode from the vertical axis was measured at the tip of the electrode and at a height of 25mm above the horizontal axis. The perpendicular distance from the tip of the electrode to the horizontal axis was also measured. For the lateral X-ray, a horizontal axis was drawn between the external auditory meatus and the orbital ridge, and a vertical axis, perpendicular to the first was also drawn through the auditory meatus. Measurements equivalent to those in the frontal x-ray were made to determine the trajectory and position of the electrode. Using these measurements, the electrode recording tracks can be reconstructed and compared.

5.6.3 Structural MRI and histology

(a) Final recording and perfusion

One monkey, Steve, was sacrificed to determine the recording sites within the brain. The other subject, Terry, is still undergoing neurophysiological recording and x-ray reconstruction evidence, only, is available.

On the final recording session, the electrode used was coated with the fluorescent marker, DiI (1, 1'-dioctadecyl-3, 3, 3', 3'-tetramethyllindocarbocyanine perchlorate, Molecular Probes Europe BV) before being lowered into the brain to help with later histological reconstruction of the electrode tracks (after Snodderly and Gur, 1995; see also Honig and Hume, 1989). At the end of the recording session, a micro-lesion (40 microamps for 40s) was made to mark the final recording site. As in all previous recording sessions, frontal and lateral x-rays were taken.

The monkey was given an injection of ketamine (to sedate it) and after 10-15 minutes a lethal dose of barbiturate (sagatal). After a few minutes the effect of the sagatal was verified by the absence of the gabella reflex (closure of the eyelids following contact with cornea).

The electrode and stereotaxic apparatus were kept in place throughout perfusion. The monkey was removed from the chair, and the thorax cut open to expose the heart. The pericardium was removed and a large bore cannula inserted into the left ventricle. The descending aorta was clamped so that the upper torso and head only was perfused. An incision was made in the right auricle to allow outflow of fluid from the circulation.

Solution was passed through the large bore cannula and into the circulation using a mechanical centrifugal pump (C16-C, Charles Ansten Pumps Ltd.). A pre-fixative wash of phosphate buffered saline and 0.2% sodium nitrate (for vasodilation) was passed through the monkey to remove blood from the system. Approximately 5 litres of solution was required to flush out all the blood. The perfusing fluid was then changed to a phosphate buffered fixative solution (4% paraformaldehyde). After approximately 5 litres of fixative was passed through the monkey, the muscles of the head and neck went rigid and perfusing was complete. The cannula was removed from the heart and the head was severed from the body.

(b) Markers for MRI

Skin and muscle was removed from around the head and it was placed in a stereotaxic frame with ear bars and orbital ridge grips. The electrode from the final recording session provided one marker to enable alignment of x-rays and structural

data from MRI. Three further markers were placed into the brain so that there were a total of two in each hemisphere. For each marker, a thin metal probe was inserted into the brain, pushed down until the base was reached and the depth relative to the dura measured. The rod was removed and a modified electrode (tungsten wire in 1mm external diameter glass tube) containing a small amount of the MRI visible solution, Magnavist (469g/ml dimeglumine gadopentetate, Schering Health Care Limited, Burgess Hill – diluted 1:50 in distilled water), inserted to the recording depth. The tubes were sealed at each end to contain the Magnavist. After the addition of each probe, further lateral and frontal x-rays were taken.

Bone cutters and a drill were used to remove the top of the skull including the implant and stainless steel wells (which are incompatible with an MRI scanner). Care was taken to ensure that all the markers remained in place.

(c) MRI

The skull was packed securely inside a 2-tesla MRI scanner (SHEFC facility, Western General Hospital, Edinburgh). A T2 coronal scan (3mm slices) was used to visualise the tissue and white and grey matter boundaries. A T1 coronal scan (800um thick slices) was used to visualise the markers placed within the brain.

(d) Histology

Bone cutters were used to remove the remainder of the skull surrounding the brain. One hemisphere of the brain was marked with a scalpel to help with later orientation. The brain was removed from the skull and sunk in successively higher

concentrations of sucrose solution (10, 20 and 30%) over a 1-month period. The brain was blocked to remove the frontal and occipital lobes. The cerebellum was left on the brain and used to form a base for sectioning. Immediately before microtome sectioning the brain was immersed in a bath of isopentane, cooled to below minus 45°C with dry ice (CO_2). After 20 minutes, the brain was removed from the isopentane and placed in the cryostat (Bright Instruments Co., Huntington, UK) at minus 14°C with the ventral surface uppermost. The brain was left for one hour to equilibrate in temperature before sectioning. Two to three sections of 25μm thickness were every 250μm and placed in bays filled with 0.1M phosphate buffer and 0.9% NaCl. A photograph of the brain block was taken every 500μm.

The sections were transferred to dishes containing water and guided onto glass microscope slides. Once dry, one section from every 250μm was stained for Nissl substance (cell bodies) and coverslipped. The remaining sections were examined for the location of DiI using fluorescent microscopy.

CHAPTER 6

TEMPORAL CORTEX AND THE OCCLUSION OF VISUAL STIMULI

6.1 INTRODUCTION

In the natural environment, objects are continually moving into and out of view. Such events may result from the movements of the object, the observer (e.g. turning the head) or other objects. Our direct perception of objects is, therefore, discontinuous yet we experience a stable environment in which objects have an existence independent of observation. Object permanence has already been discussed in chapter 3 and will not be covered in detail here.

Macaques and other primates are highly social animals and the movements and locations of conspecifics are very important in structuring behaviour. Macaques live in hierarchical groups and visual and auditory social signals (e.g. threat, submission) are critically important. The interpretation of such signals (e.g. whether it is directed at you or not) may depend on the relative locations of conspecifics, even if out of sight or partially occluded.

As described in chapters 3 and 4 there is much evidence to suggest that non-human primates maintain representations of objects that are out of sight. They are aware of the presence and nature of objects that are hidden from view, but fail on stage 6 object permanence tasks suggesting that they are unable to represent the unseen movements of objects. Dumas and Brunet (1994) have suggested that the failure of non-human primates on invisible displacement tasks may be partly

attributable to the use of inanimate objects in such tasks. With socially relevant, animate objects (e.g. conspecifics), different results might be obtained. Primates may have a special aptitude for dealing with problems with a social content (for review, see Anderson, 1998). On computerized tasks, there is some evidence for the ability to represent hidden movements in macaques (Filion *et al.*, 1996) but only in subjects that had received extensive training (see chapter 3).

This knowledge about occluded objects may be expressed at a cellular level. In IT cortex it has been shown (Kovacs *et al.*, 1995) that neurones retain their selectivity for static stimuli under partial occlusion (e.g. a stimulus partially occluded by a series of regularly spaced bars). Despite this maintained selectivity, response strength was seen to decrease with increasing degree of occlusion. In these experiments, however, there was a time lag between the presentation of the occluding pattern and occluded shape increasing the level of perceptual segregation (Vogels and Orban, 1996). It is unknown whether the selectivity would remain with simultaneous presentation of the occluder and stimulus.

In posterior parietal cortex, Assad and colleagues (Assad and Maunsell, 1995; Eskandar and Assad, 1999) have reported activity related to inferred motion. For example, Assad and Maunsell (1995) presented monkey subjects with a moving dot on a visual display, which disappeared. On some trials (so called "blink" trials) the dot reappeared after a delay at the same location and no motion could be inferred during the period of absence. On other trials, the dot reappeared at a displaced location consistent with its initial trajectory and, in these trials, motion of the stimulus during its absence could be inferred. The different trials were presented in blocks. Greater cell activity was observed in the inferred motion trials than in the blink trials during the period of absence of the stimulus. This activity was always

less than that observed in response to visible motion of the stimulus. In individual trials, there was no intrinsic information at the moment of disappearance from which to infer motion or continued existence - there was no occluding screen and no gradual occlusion of the stimulus. On a given trial, at the moment of disappearance, continued motion could be inferred only from the blocked nature of the trials.

In areas MST and 7a (PG), at the caudal end of the superior temporal sulcus, cells responsive during the visual tracking or pursuit of a moving target have been found to continue firing during the brief disappearance (up to 1s) of the target (Newsome *et al.*, 1988; Sakata *et al.*, 1983). The subjects maintained tracking during this period. Such activity has been interpreted as evidence of an extraretinal input to the cells related to the eye movement itself and not to the visual stimulus.

Stimuli also disappear from sight when the illuminating light is extinguished. In the premotor cortex (area F4), cells respond to objects in close peri-personal space (<1.0m) and may enable the sensory guidance of motor movements (Fogassi *et al.*, 1996; Graziano *et al.*, 1997b). Such cell activity has been shown to persist in the dark (Graziano *et al.*, 1997a). It is not known, however, whether the activity persists under natural occlusion, a situation in which the actions required to interact with the hidden object would be altered.

Cells in STSa have been found to code the movements of objects into and out of view. Perrett *et al.* (1985) found transient responses to stimuli moving out of view behind an occluding surface (exit) and conversely to the movement of stimuli out from behind an occluder and into view (entry). The stimuli were presented briefly (1-2 second duration) using a large aperture shutter. For example, the cell illustrated in figure 6.1 responded to objects moving out of view, but not into view, and there was no response to equivalent movements fully in-view. Many cells were found to be

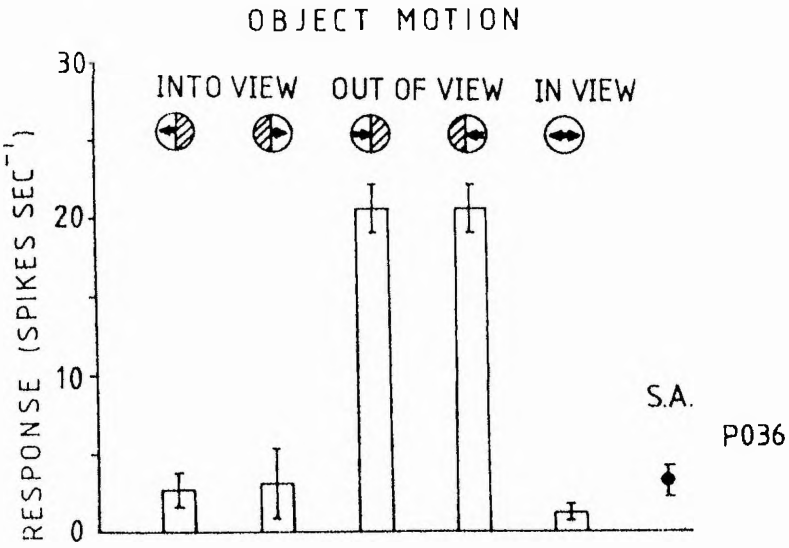


Figure 6.1 Responses of one cell to objects moving out of view. Mean and standard error are illustrated. The cell showed significant responses, compared with spontaneous activity (SA), to lateral movements of the object in which the object was gradually occluded. Movements of the object into view, and movements fully in-view failed to elicit significant responses. The cell was not directionally selective, responding to leftward or rightward movements as long as the objects were moving out of view (from Perrett *et al.*, 1985).

selective for the direction of motion, but the position of the movement within the visual field was found to be unimportant.

There was no data on the nature of cellular responses in STSa during periods of complete occlusion. Perrett *et al.* (1985) presented stimuli briefly and recorded transient responses to exit and entry. They did not record responses for any appreciable time following the exit of stimuli from view. Exit and entry are often linked events. Occlusion may be only temporary and entry may predictably follow exit from view. The experiments reported here used the same stimuli of objects moving out of sight as Perrett *et al.* (1985). A continuous sequence of events was presented over a long time course, however, in which stimuli moved out of sight and then entered back into view after a period of complete occlusion. Neuronal responses were recorded throughout this period.

The aim of the study was to investigate potential neural mechanisms for maintaining a representation of objects that are hidden from view.

6.2 METHODS

6.2.1 Experimental methods

Cells were tested clinically as described in general experimental methods (see chapter 5). Any cells showing changes in activity levels as the experimenter moved around the laboratory were tested more extensively. Cell responses were recorded as the experimenter or other objects moved around the laboratory, out of view at different positions and subsequently back in to view after a variable period of complete occlusion (lasting 3-20 seconds). Figure 6.2 shows a plan view of the

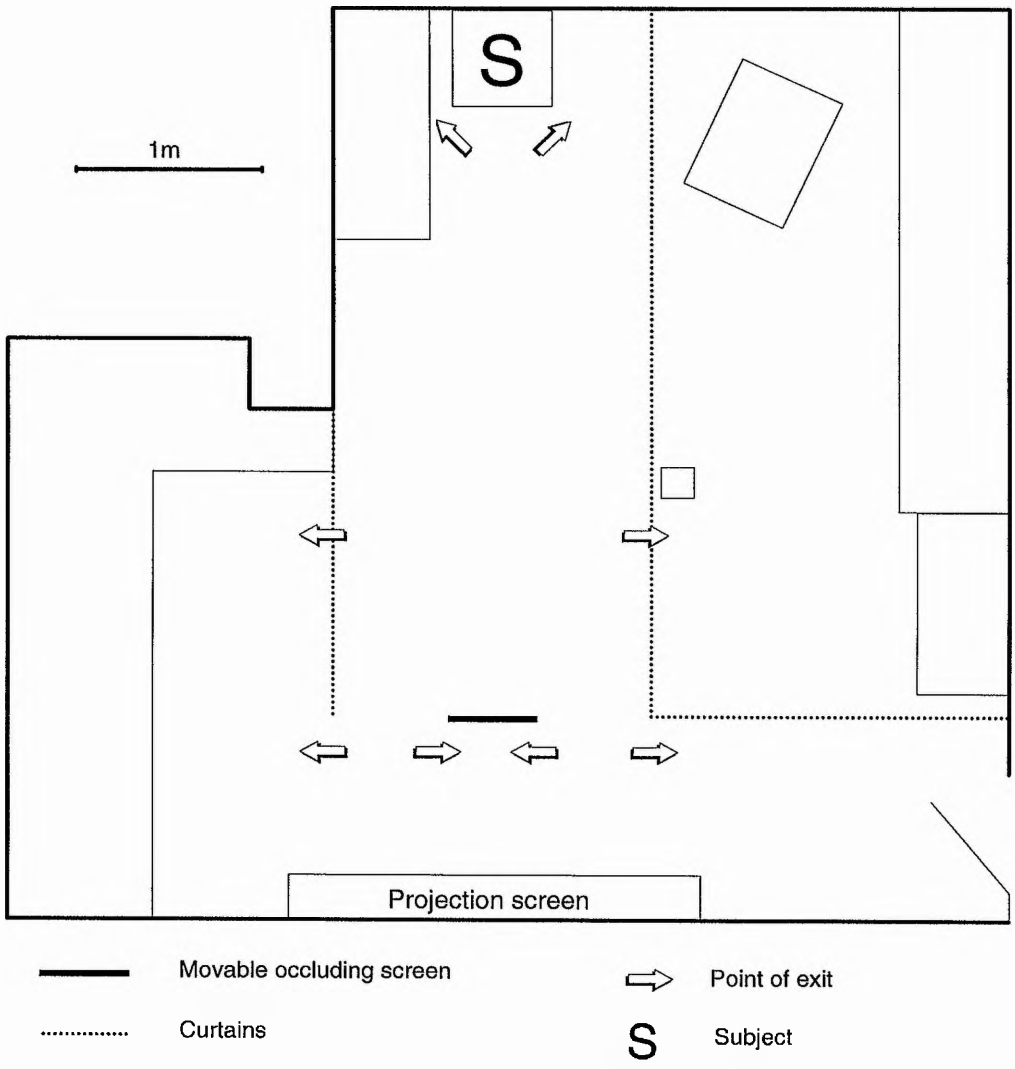


Figure 6.2 Scale plan view of the laboratory with the principal points at which occlusion was tested indicated.

laboratory with the principal testing locations indicated. For occlusion close to the monkey, the sides of the primate chair acted as the occluding surface. In all other cases the occluding surfaces were either curtains, a wooden door (central occluder) or cardboard sheeting. As well as these principal sites, the central occluder and cardboard sheeting could be moved to any location in the room. The position of the curtains was fixed, although the point of exit (gap between adjacent curtains) could be altered. In most cases the central occluder was not present when occlusion at the sides of the laboratory was being tested. The visual stimulus resulting from the movements of objects being occluded and reappearing can be divided into five distinct phases (see figure 6.3):

(1) Pre-occlusion - object moved towards the occluder. The object was in sight throughout this period.

(2) Occlusion - object was gradually occluded as it moved behind the occluder.

(3) Out-of-sight - object was completely occluded from view. In this phase only the occluder was visible.

(4) Reappearance - object moved back into view, being gradually revealed. Movement in this phase was either in the same direction as the pre-occlusion movement or in the opposite direction depending on whether the occluder was at the side (left or right) or centre of the laboratory.

(5) Back-in-view - the object was completely in view again and the trial ended with the object static at its starting position.

Speed of movement was kept constant at a rate of approximately 0.75m/s. Duration of the occlusion phase from the time the first part of the body (the leading foot) was occluded until the time when no part of the body could be seen was

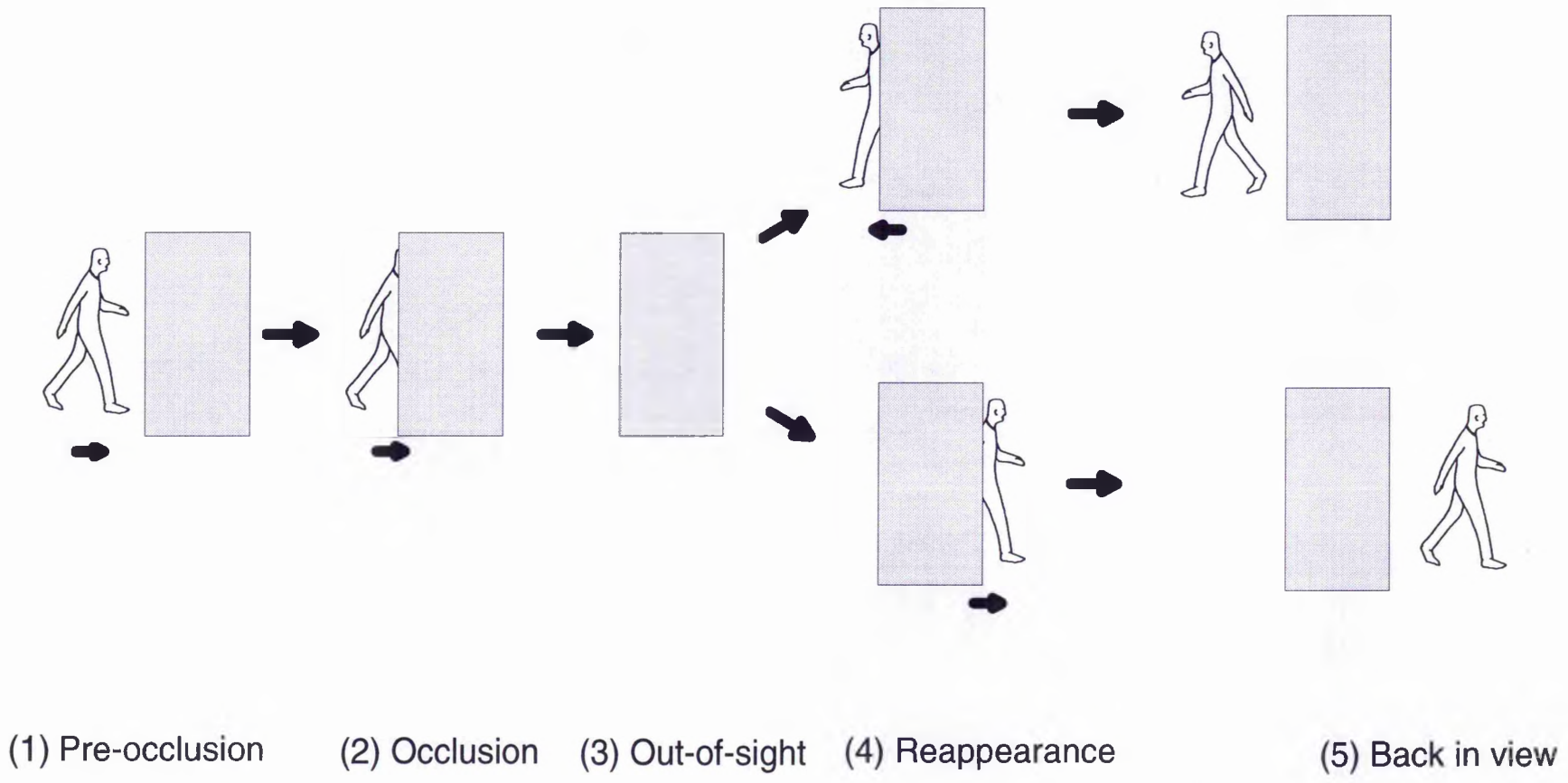


Figure 6.3 Phases of the visual stimulus. The object (experimenter) moved towards the occluder (1), was gradually occluded (2) and came back into view (4, 5) after a period of complete occlusion (3). With central occlusion the direction of movement on reappearance was the same as the direction of pre-occlusion movment. For lateral occlusion, however, the direction of movement on reappearance was in the opposite direction to pre-occlusion movement. Large arrows show the progression of the stimulus, small arrows, the direction of movement.

approximately 0.5s. The duration of the reappearance phase was similarly approximately 0.5s.

Cells were tested with occlusion at different locations, and with different objects. The principal object used in testing was the experimenter. For other objects the experimenter remained in view and the objects (e.g. mobile chair) were moved out of sight behind an occluder. This was achieved either by pushing the object or by pulling on a piece of string attached to the object.

Trials were presented in a pseudo-random order with interleaving of the different stimulus conditions. All testing was filmed from the monkey's perspective with a video camera located above the head of the subject.

Subjects were not required to perform a fixation task as this would be difficult to train for fixation during the entire test period (9 - 25 seconds; see Graziano *et al.*, 1997a). Eye movements were recorded during testing with an infra-red camera mounted on the side of the primate chair. This signal was integrated (Panasonic VHS video mixer, WJAVE7) or synchronised (VITC time-code generator and frame counter, Horita VG50) with the room view of stimulus events.

6.2.2 Data analysis

Cell activity was analysed offline from the video recordings made during testing. The activity was divided into 1 second bins and aligned independently with both occlusion and reappearance. The first three phases aligned with occlusion will be referred to as the "occlusion sequence". Similarly, the last three phases aligned with reappearance will be referred to as the "reappearance sequence". Both sequences include activity in the out-of-sight phase, but aligned either with respect to

the occlusion phase or the reappearance phase. Since the duration of the occlusion and reappearance phases was less than 1 second each, these phases occupy a single bin. Mean cell responses (minimum 4 trials) were analysed using repeated-measures ANOVA with time bin as a factor (using the Greenhouse-Geisser adjustment where appropriate). This analysis avoids noise that might have been introduced as a result of inter-trial variation in the neurones' intrinsic firing rate. Cell activity at 3 seconds pre-occlusion was taken as a measure of pre-occlusion activity for all statistical comparisons except in cells where this data was not available. In these cases, cell activity at 2 or 1 second pre-occlusion was used for comparison. The occlusion sequence was analysed using data from up to 3 seconds pre-occlusion until the end of occlusion. Responses during reappearance were analysed only for those cells for which data at 3 seconds pre-occlusion was available. The reappearance sequence was analysed across the time period from 2 seconds before reappearance until 2 seconds after reappearance with the cell activity at 3 seconds pre-occlusion as an additional level for comparison with pre-occlusion activity. Post-hoc Newman-Keuls testing (with level of significance $p<0.05$) was used to evaluate significant differences in firing across the different time bins for analysis of both the occlusion and reappearance sequences.

For cells that were recorded from 3 seconds pre-occlusion until 2 seconds after reappearance, an average response (population response) was calculated. Responses were first normalised according to the following equation:

$$\text{Normalised response at time bin, t } (N_t) = \left(\frac{x_t - PRE_{\min}}{OCC_{\max} - PRE_{\min}} \right) \times 100$$

Where x_t is the average cell response at time bin, t; PRE_{min} is the minimum average pre-occlusion response for that cell; and OCC_{max} is the maximum average response during the occlusion sequence (phases 1-3) for that cell.

This normalisation returns the average response for a cell at a given time bin (t) as a percentage of the range of activity observed. The population response was obtained by averaging the normalised responses for each cell at each time bin.

6.3 Results

6.3.1 Overview

Out of 463 cells recorded in STSa, 274 showed visual responsiveness and of these 33 (12%) showed elevated levels of activity in the out-of-sight phase relative to pre-occlusion levels.

To give an overview of the response pattern of these 33 cells, the population response will first be described followed by separate analyses of the occlusion and reappearance sequences. More specific results will also be discussed including justification and brief discussion of some tests that were performed in the course of the investigation.

6.3.2 Population response

The responses of 26 neurones were recorded from 3 seconds pre-occlusion until 2 seconds after reappearance (minimum 3 trials), and these neurones were used

to form a population response (Figure 6.4*). This population response shows many of the typical features of the neuronal responses recorded. There is some increase in activity as the experimenter moves towards the occluder, with the response increasing rapidly during the occlusion phase and reaching a peak in the first second following complete occlusion (occlusion sequence: $F_{2.4, 59.8} = 26.5$, $p<0.0001$). After 6 seconds post-occlusion, cell activity is still elevated above pre-occlusion levels ($p<0.03$ Newman-Keuls post-hoc test). On reappearance (reappearance sequence: $F2.7, 68.7 = 8.5$, $p<0.0001$) the population response is a small but significant ($p<0.04$ Newman-Keuls post-hoc test) increase in activity before levels drop back to their pre-occlusion state.

6.3.3 Occlusion sequence

(a) Time course

Considering the occlusion sequence in isolation, 2/33 neurones showed peak levels of activity prior to occlusion, 4/33 during occlusion and the remaining 27/33 cells showed their peak levels of activity in the out-of-sight phase with only the occluder visible. Latency to peak activity in these 27 cells varied from 1 to 4 seconds post-occlusion. Figure 6.5 shows the response of three cells with different time courses of activity. For all three cells, activity in the out-of-sight phase is elevated relative to pre-occlusion levels. Cell S97_2481a (occlusion sequence: $F_{3.2, 12.9} = 13.0$, $p<0.001$) shows its peak level of activity just before occlusion, cell T12_3130 (occlusion sequence: $F_{3.8, 18.8} = 9.2$, $p<0.0003$) just after occlusion, and cell

* On this and all subsequent graphs, error bars show the standard error of the means.

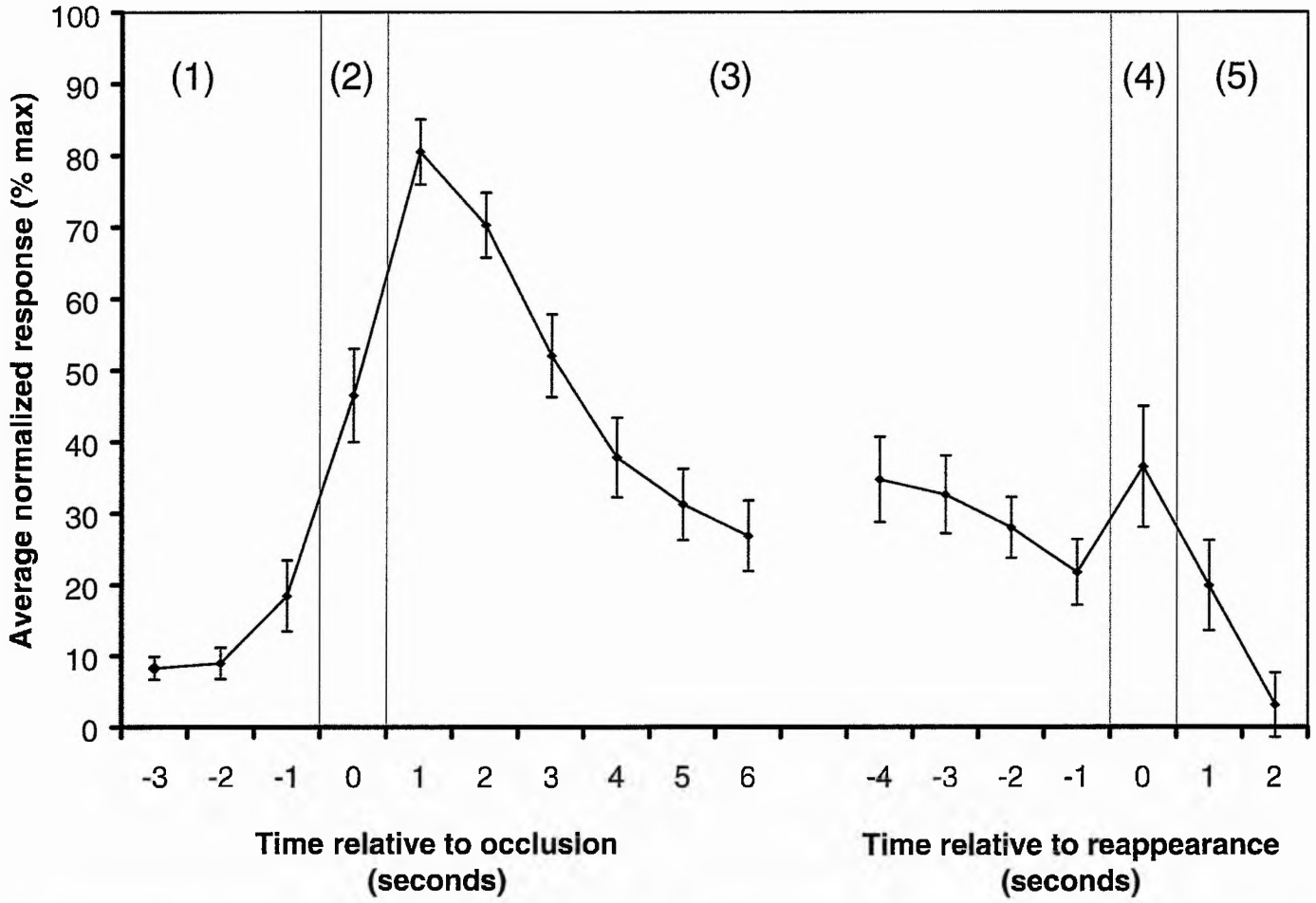


Figure 6.4 Average response (population response) for 26 neurons recorded from 3 seconds pre-occlusion until 2 seconds after reappearance. The numbers at the top of the graph refer to the phases of the visual stimulus as defined in the text and figure 6.3.

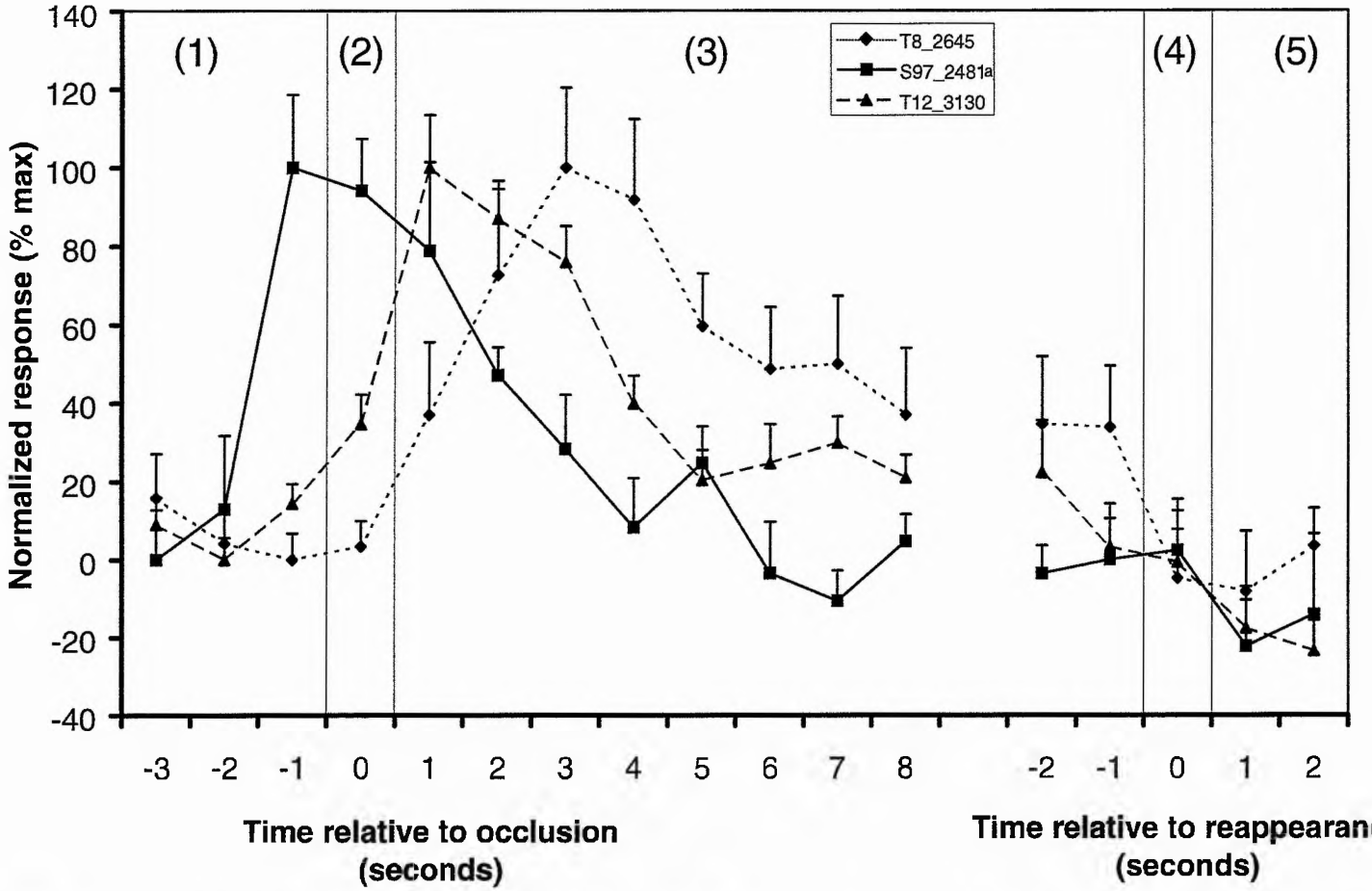


Figure 6.5 Time course of individual neuronal responses. All three cells show a qualitatively similar pattern of change in activity but with different time courses with respect to occlusion. For each cell activity remains elevated above pre-occlusion levels in the out of sight phase (3). T8_2645, n=10; S97_2481a, n=5; T12_3130, n=8.

T8_2645a (occlusion sequence: $F_{2.9, 26.2} = 5.3$, $p<0.01$), 3 seconds into the out-of-sight phase. Despite the differences in latency to peak response, all three cells show a qualitatively similar pattern of activity change over time.

(b) Duration

The duration of the responses in the out-of-sight phase was examined at both the individual cell and population level.

Individual estimates of the duration of cell responses in the out-of-sight phase were calculated for those cells recorded from at least 3 seconds pre-occlusion. These were the cells whose responses were included in the population response (Figure 6.4). The presence of a response was defined by statistically significant activity (Newman-Keuls post-hoc testing) at a given time bin in the out-of-sight phase compared with activity at 3 seconds pre-occlusion. The resulting estimates of response duration varied from 1 to 11 seconds post-occlusion, with mean duration 3.4s, and median 2.5s. Figure 6.6 shows the distribution of out-of-sight response duration for the cells included in the population response.

Similar analysis on the population response shows that at 6 seconds post-occlusion cellular activity is still elevated relative to pre-occlusion levels (see section 6.3.2). Regression and extrapolation (Statistica 4.5, StatSoft Inc., 1993) were used to determine when the population response would return to pre-occlusion levels. The average normalised responses for 1 to 6 seconds post-occlusion were log-transformed and regressed against time (see figure 6.7). Extrapolating the regression line produces an estimate of 10.6 (range 9.6-12.3) seconds before post-occlusion activity returns to the activity level at 3 seconds pre-occlusion.

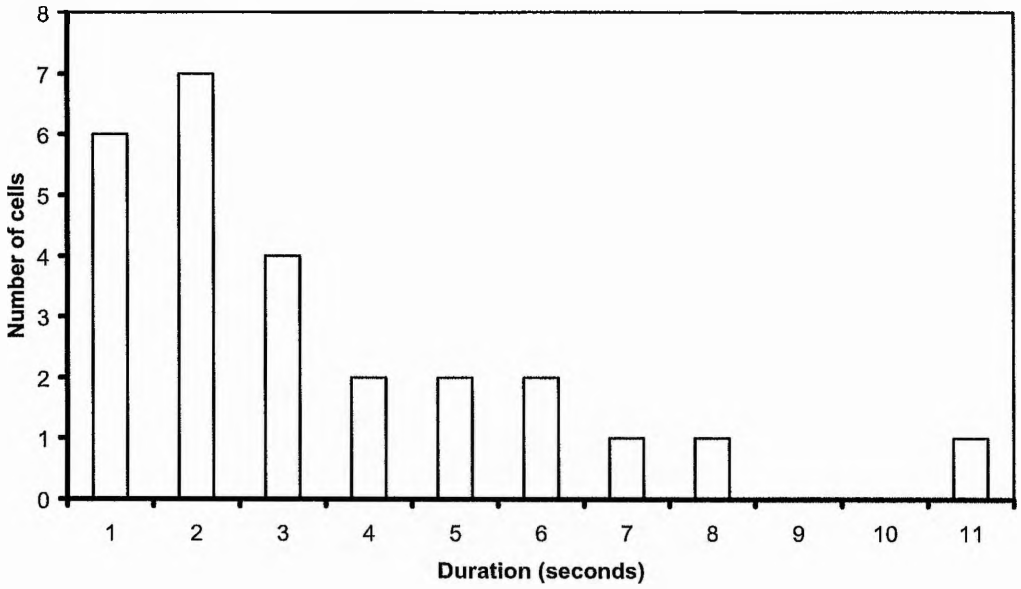


Figure 6.6 Histogram of the duration of cell responses in the out-of-sight phase. Duration is defined as significance in post-hoc Newman-Keuls tests compared with activity at 3 seconds pre-occlusion.

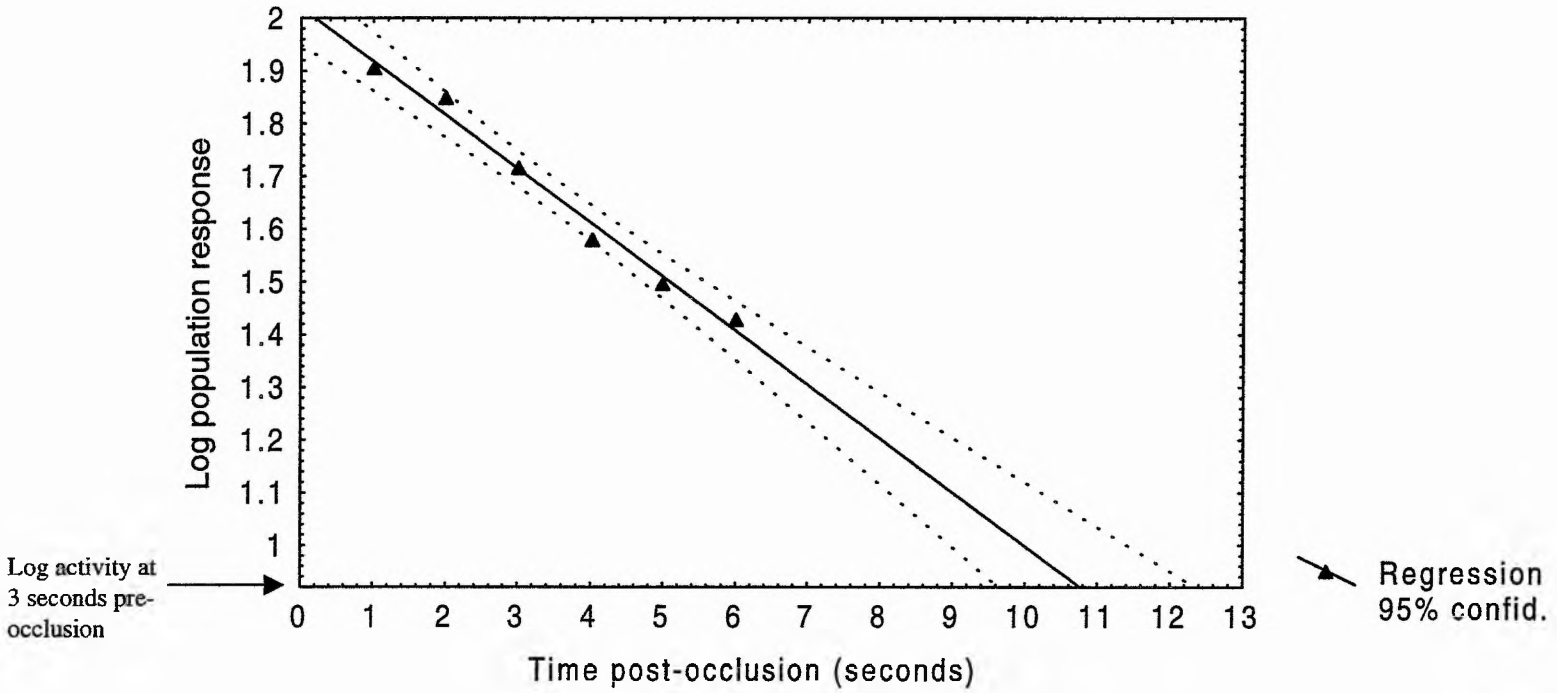


Figure 6.7 Regression of the log transformed population response against time. Extrapolation of the regression line suggests that the population activity remains elevated above pre-occlusion levels until 10.7 seconds post-occlusion. The 95% confidence limits for the line give a range of 9.6-12.3 seconds for the activity to return to pre-occlusion levels.

(c) Positional selectivity

Selectivity for the position of the occlusion within the laboratory was observed in all 30/30 cells tested. Most cells (24/30) showed differential activity according to the side of the occlusion within the laboratory. For the cell illustrated in figure 6.8, occlusion on the left side of the laboratory produced greater excitation in the out of sight phase than occlusion on the right side of the laboratory (relative to pre-occlusion levels). In this instance, however, both position of occlusion and direction of approach varied between the two conditions. Leftward movement preceded occlusion on the left side of the laboratory and rightward movement preceded occlusion on the right side of the laboratory. Activity in the out of sight phase elicited by occlusion in the centre with preceding leftward movement is significantly less than activity elicited by occlusion on the left (figure 6.8). A further interpretation is that the activity observed during the out of sight phase reflects anticipation of the direction of movement on reappearance. Out of the three conditions so far discussed, occlusion on the left is the only one in which the direction of movement on reappearance is rightward. The selectivity of this cell, however, cannot be explained by the direction of movement following occlusion. The activity in the out of sight phase elicited by central occlusion with rightward movement both preceding and following occlusion is significantly less than that elicited by occlusion on the left. Thus, the activity in the out of sight phase for this cell appears to represent selectivity for the position of occlusion and cannot be explained by selectivity for the preceding movement or anticipation of the upcoming movement.

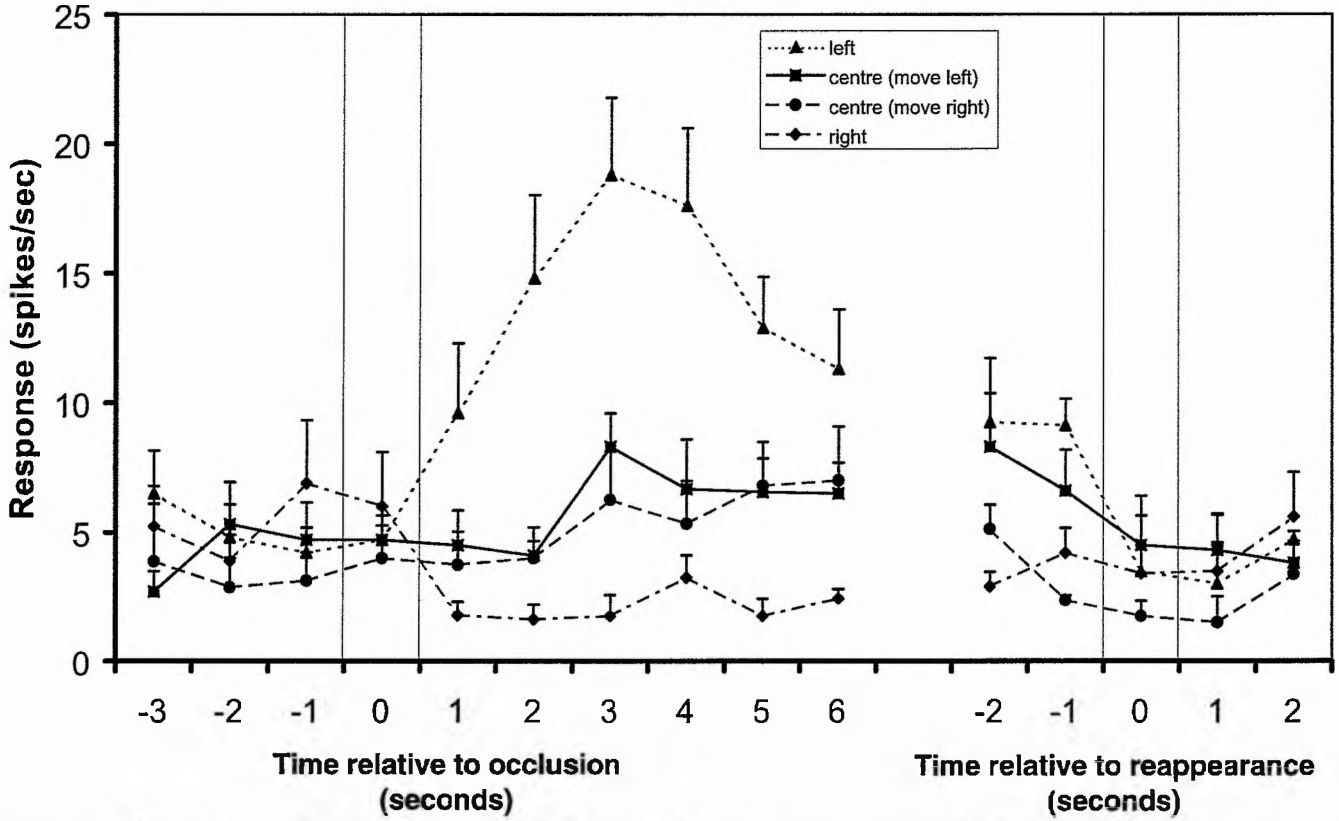


Figure 6.8 Responses of a single neuron to occlusion at different positions within the laboratory. The activity of this neuron was dependent on the position of occlusion within the laboratory and not on the direction of approach or emergence. 2-way repeated measures ANOVA with time as a within-subjects factor and condition (left; centre, move left; centre, move right; and right) as a between-subjects factor shows a main effect of both time ($F=4.37$, $df=3.5, 97.8$, $p<0.01$) and condition ($F=9.24$, $df=3, 28$, $p<0.005$) with a significant time by condition interaction ($F=4.13$, $df=10.5, 97.8$, $p<0.0001$). Occlusion on the left elicited significantly greater activity ($p<0.05$) in the out of sight phase than all other conditions. Pre-occlusion cell activity did not differ significantly between the conditions ($p>0.05$). Left, n=10; centre, move left, n=9; centre, move right, n=8; right, n=9.

Selectivity for the position of occlusion that was not dependent on direction of approach was observed in 19/30 cells. This direction-independent positional selectivity was manifest either as a difference in response between near (distance = 1-2m) and far (distance = 3-4m) occlusion (n=13, e.g. fig 6.9), or between lateral and central occlusion (n=9 e.g. fig 6.8) with the same direction of approach (as discussed above). For the neurone illustrated in fig 6.9, the activity in the out of sight phase elicited by occlusion of the experimenter at a distance of 4m from the monkey was greater than the activity elicited by occlusion of the experimenter 1.5m away. For both distances, the direction of movement preceding and following occlusion was identical.

Spatial position can be coded in terms of either an egocentric or an allocentric frame of reference (see chapter 2). For a given cell with spatial sensitivity, the distinction between egocentric and allocentric coding can be determined by moving the subject (for example, see Tamura *et* al., 1990, 1992; Feigenbaum and Rolls, 1991). Egocentric coding implies that spatial position is coded relative to the location of the subject. If the monkey is moved, the area of positional sensitivity of the cell should move an equivalent distance, thus remaining at the same position relative to the subject. On the other hand, allocentric coding implies that spatial position is coded relative to cues or landmarks external to the subject (e.g. relative to the four walls of a room). Such coding implies positional sensitivity independent of the location of the subject. If the subject is moved the area of sensitivity of the cell should not move but remain at the same location in space relative to the available external cues.

For one of the cells described in this chapter, responses to occlusion were measured with the monkey in different spatial positions. The positional sensitivity of

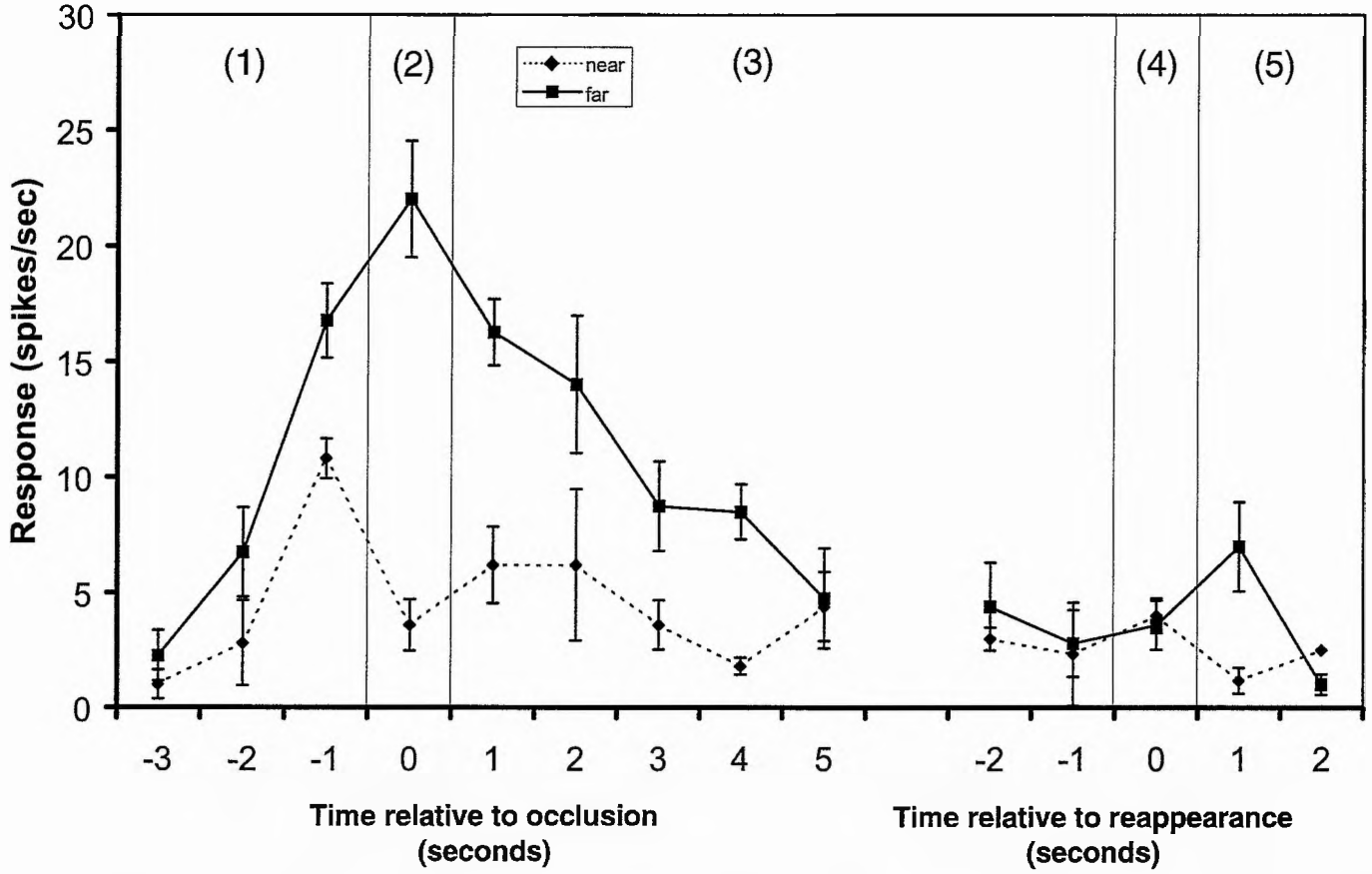


Figure 6.9 Responses of a cell to occlusion at different distances. Near = 2.5m, far = 4m. Occlusion sequence: 2-way ANOVA with time as a within-subjects factor and distance as a between subjects factor shows a main effect of both distance ($F_{1, 7} = 84.9$, $p<0.0001$) and time ($F_{2.7, 18.6} = 11.3$, $p<0.0002$) with a significant distance by time interaction ($F_{2.7, 18.6} = 4.5$, $p<0.02$). Post-hoc testing shows significant differences between the responses for the two distances at 0, 1 and 2 seconds relative to occlusion. There is no difference between the responses in the pre-occlusion phase. Near, n=6; far, n=5.

this neurone has already been illustrated in figure 6.9. The cell responded more following occlusion of the experimenter at a distance of 4m from the subject (far) than following occlusion of the experimenter at 1.5m from the subject (near). To elucidate the spatial frame of reference, the responses of this neurone were recorded with the monkey in two different spatial positions relative to the back wall of the laboratory: 0m (normal position) and 2.5m (see figure 6.10). If the neurone was coding space in an egocentric reference frame, the response to occlusion of the experimenter at 4m with the monkey at 2.5m should be the same as the response to occlusion of the experimenter at 1.5m with the monkey at 0m. In both cases the occlusion event occurs at a distance of 1.5m from the subject. If the neurone was coding space in an allocentric reference frame, however, the response to occlusion at 4m with the monkey at 2.5m should be the same as the response to occlusion at 4m with the monkey at 0m. In both cases, the occlusion event occurs at the same spatial position relative to the room landmarks. The results obtained are illustrated in figure 6.11. The response is the same regardless of the spatial position of the subject. Furthermore, the response elicited by occlusion of the experimenter at 4m with the subject at 2.5m is qualitatively different to that obtained with the monkey at 0m and the occlusion of the experimenter at 1.5m (figure 6.9), a situation with equivalent distance between the subject and the site of occlusion. These results suggest the allocentric coding of spatial position.

(d) Form selectivity

Selectivity for form was found in 10/15 cells tested. These cells showed differential activity following the occlusion of different objects. The majority of

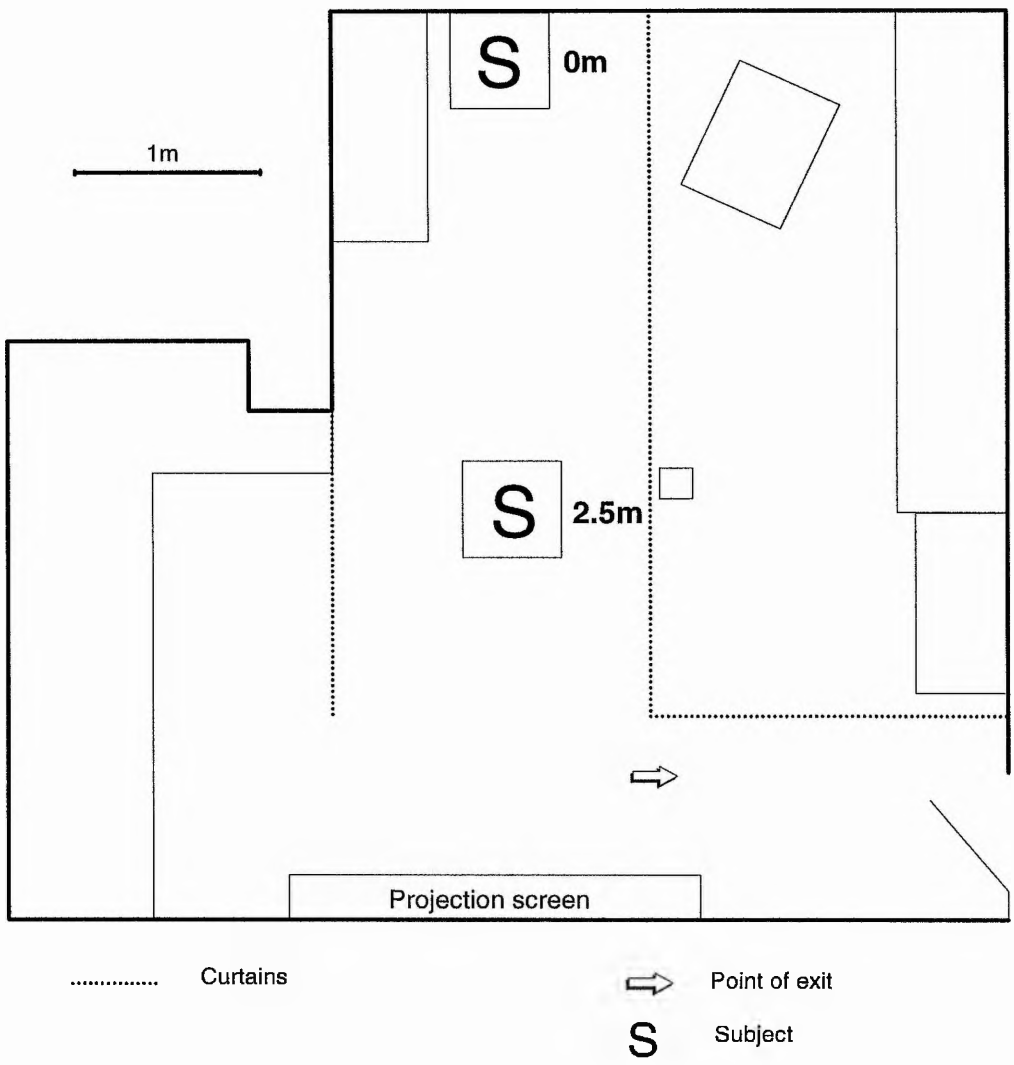


Figure 6.10 Plan view of the laboratory showing the two positions of the monkey used in testing the spatial frame of reference of a cell responsive to occlusiion on the left side of the room. The results of testing are shown in figure 6.11.

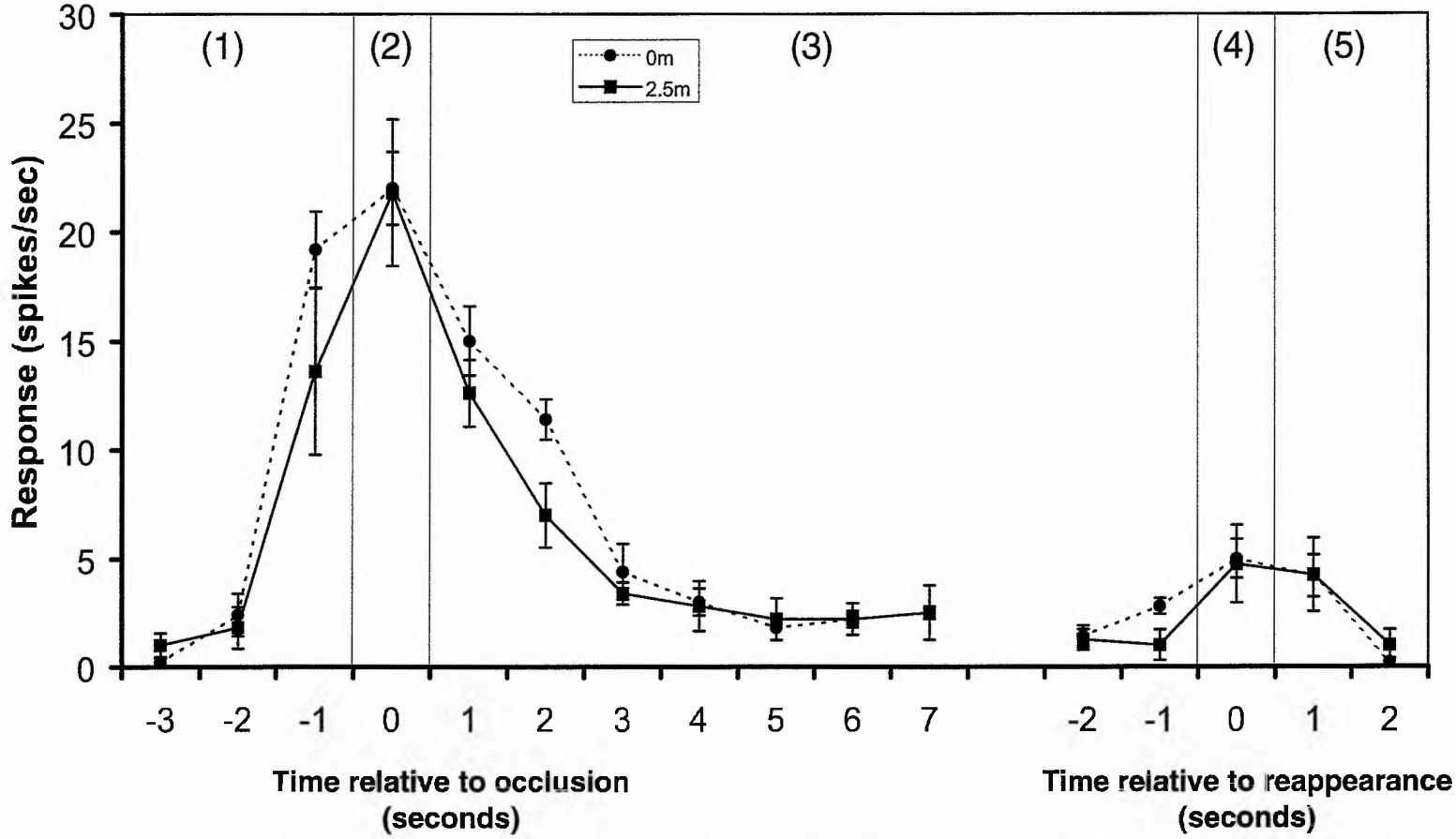


Figure 6.11 Responses of the same cell as in figure 4.8 to occlusion at 4m with the monkey at 0m or 2.5m. The responses of the cell are suggestive of allocentric coding of space. Occlusion sequence: 2-way ANOVA with time as a within-subjects factor and position of monkey as a between-subjects factor shows a mian effect of time ($F_{2.7,\ 21.8} = 47.5$, $p<0.0001$), but no effect of position ($F_{1,\ 8} = 3.6$, $p>0.05$) and no time by position interaction ($F_{2.7,\ 21.8} = 0.97$, $p>0.05$). Each condition, n=5.

these cells (9/10) showed greater responses to the experimenter moving out of sight than other objects. The neurone illustrated in figure 6.12 showed an increase in activity in the out-of-sight phase following occlusion of a mobile television stand. Following occlusion of the experimenter at the same location, however, there was no change in activity levels. This apparent form selectivity is unlikely to be due to the continued visibility of the experimenter during the testing of objects other than the experimenter. For 8/8 cells tested, the presence of one experimenter in view did not affect the response to a second experimenter moving out of sight.

(e) Auditory responses

Auditory responses were not explicitly tested in all the cells recorded, but 7 cells were observed clinically to respond to auditory stimuli. Auditory stimuli tested included experimenter produced sounds (e.g. tapping foot on the floor, imitation monkey calls, and the sound of different objects being struck together) and computer-generated tones. Auditory responses were observed only in the out-of-sight phase when the experimenter was not visible. When the experimenter was in sight, the responses were either very small or completely absent. In comparison with the responses elicited by the visual stimulus of the experimenter moving out of sight, auditory responses were transient in nature and unaffected by the length of time following occlusion.

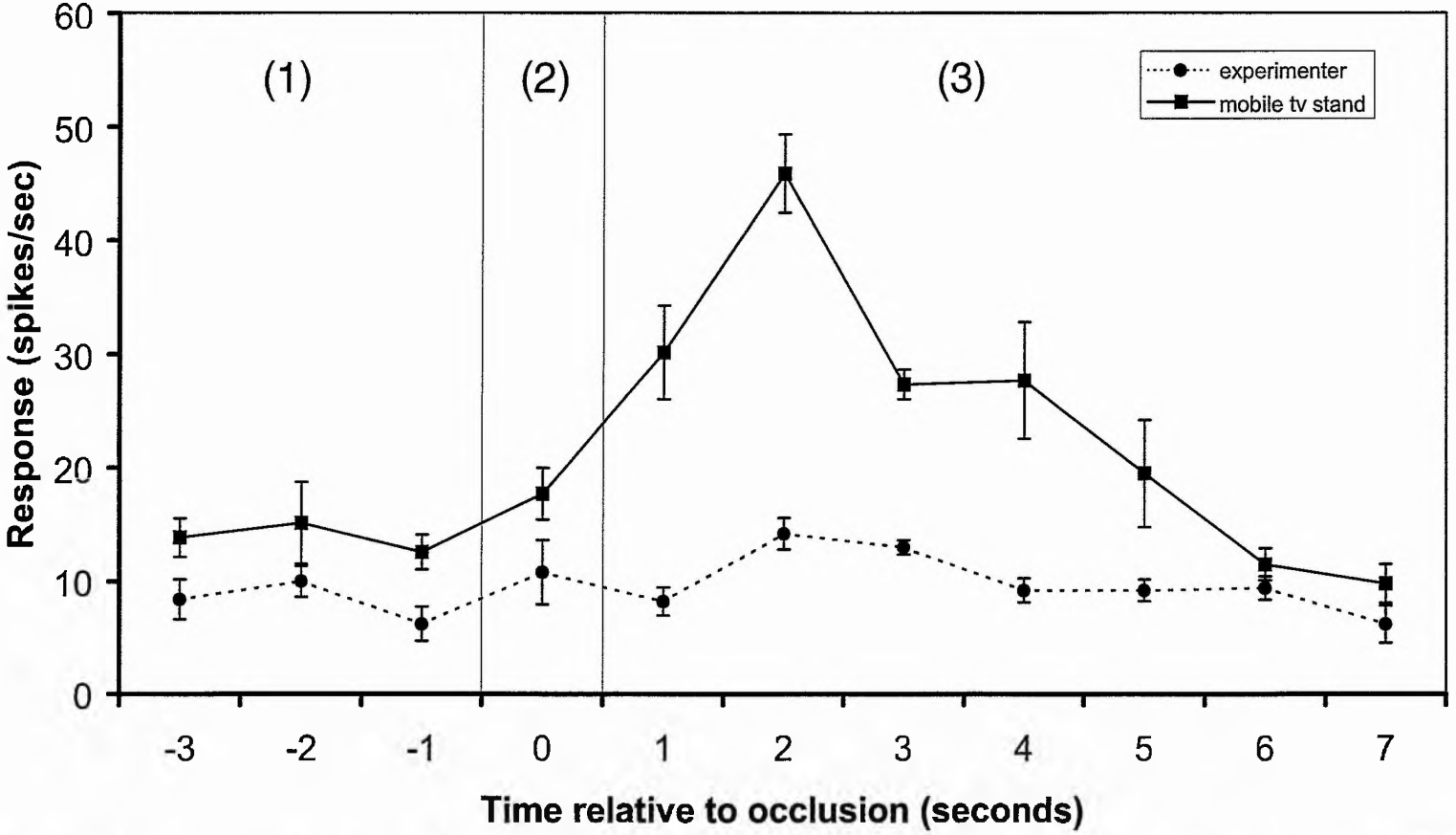


Figure 6.12 Responses of a cell to the occlusion of different objects. The cell shows a differential response between a mobile TV stand moving out of sight and the experimenter. 2-way ANOVA with time as a within-subjects factor and object as a between-subjects factor shows a main effect of both object ($F_{1, 9} = 96.6$, $p<0.0001$) and time ($F_{3.8, 34.2} = 10.3$, $p<0.0001$) with a significant object by time interaction ($F_{3.8, 34.2} = 5.3$, $p<0.002$). Post-hoc testing shows significant differences between the responses at 1, 2, 3 and 4 seconds relative to occlusion. There are no differences between the responses in the pre-occlusion phase. Each condition, n=5.

(f) Nature of disappearance

Movement of an object out of sight is only one way that an object might disappear from view. For five neurones, the selectivity for the manner of disappearance was tested. Specifically, the neurones were tested with movement of an object out of sight (involving gradual occlusion of the object) and sudden disappearance of the object (produced by closing an LCD shutter placed close to the monkey's head - see chapter 5). The shutter has a rapid rise time (<15ms) and closure of the shutter leads to the disappearance of an object from view without gradual occlusion. Many cells were found not to respond when the shutter box was attached to the chair (probably due to the restricted field of view removing spatial cues) and only a small number of cells could be tested in this manner. There were two trial types: (a) occlusion - the shutter box opened and the experimenter moved out of sight behind an occluder. The experimenter started very close to the occluder and the visual stimulus largely corresponds to the occlusion and out-of-sight phases described in the methods. The shutter was open for a total of 5 seconds; (b) shutter closing - the shutter opened to reveal the experimenter static at the position of occlusion used in the occlusion trial, but fully in view. The shutter was open for approximately 1 second (equivalent to the time taken for the experimenter to move out of sight in the occlusion trial) and then closed.

In both conditions the experimenter disappeared from view. In the occlusion trial the experimenter disappeared through gradual occlusion whereas in the shutter trial the experimenter disappeared suddenly through the spontaneous occlusion of the entire field of view. Out of the 5 cells tested, 4 (80%) responded differentially between the two trial types, showing greater changes in activity in the occlusion

trials than in the shutter trials. The cell illustrated in figure 6.13 is typical of these cells. There was an increase in activity following movement of the experimenter out of sight, but no change in activity if the experimenter disappeared at the same location through the closure of the shutter box. The remaining cell showed equivalent responses in both the occlusion and shutter trials - an increase in activity following disappearance of the experimenter from view.

6.3.4 Reappearance sequence

Only those 26 cells that were included in the population response had sufficient data for analysis of responses during the reappearance sequence.

Reappearance responses for the preferred occlusion location could be grouped into three categories according to the direction of significant changes in activity levels: (a) increase (9/26), e.g. figure 6.14, cell S90_2411b ($F_{2.9, 20.4} = 31.8$, $p<0.0001$); (b) decrease (2/26) to baseline or below e.g. figure 6.5, cell T12_3130 ($F2.6, 15.5 = 8.3$, $p<0.002$); and (c) no change (15/26), e.g. Figure 6.14, cell S90_2411a ($F_{1.8, 12.5} = 0.89$, $p>0.05$). For three neurones, peak activity for the entire duration of the visual stimulus was seen during this reappearance phase. For 2 cells the activity on reappearance depended on the position of the occlusion and subsequent position and direction of reappearance within the laboratory.

In comparison with the occlusion sequence responses, changes in activity during the reappearance sequence were of much shorter duration, and in the majority of cases (23/26), smaller in magnitude.

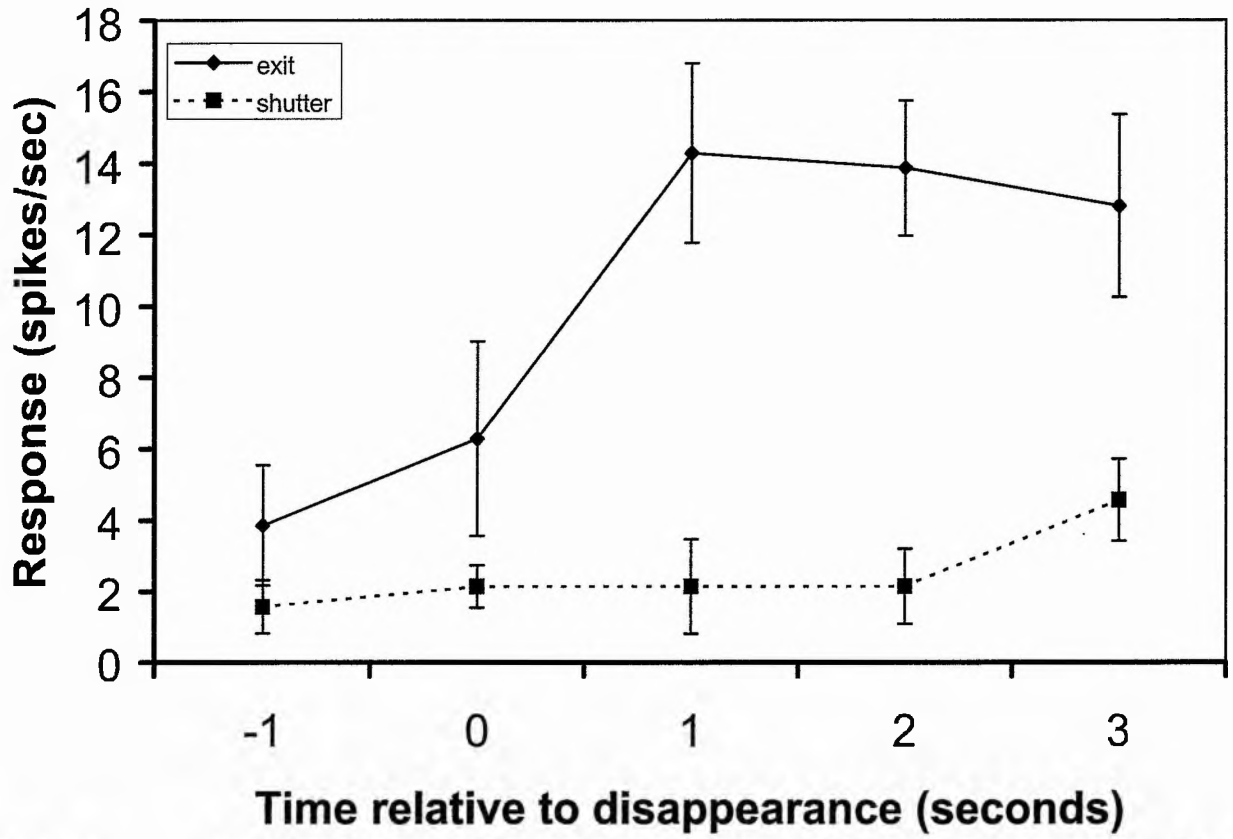


Figure 6.13 Responses of a cell to disppearance of the experimenter through gradual occlusion (moving out of sight) or closure of the shutter box. In both conditions the experimenter was in sight for one second before disappearing completely from view. 2-way ANOVA with time as a within-subjects factor and manner of disappearance as a between subjects factor shows a main effect of both the manner of disappearance ($F_{1, 10} = 37.3$, $p<0.0002$) and time ($F_{2.3, 22.9} = 6.3$, $p<0.01$) with a significant interaction between the two factors ($F_{2.3, 22.9} = 3.8$, $p<0.05$). Post-hoc testing shows significant differences between the two responses at +1, 2 and 3 seconds relative to disappearance. Exit, n=7; shutter, n=7.

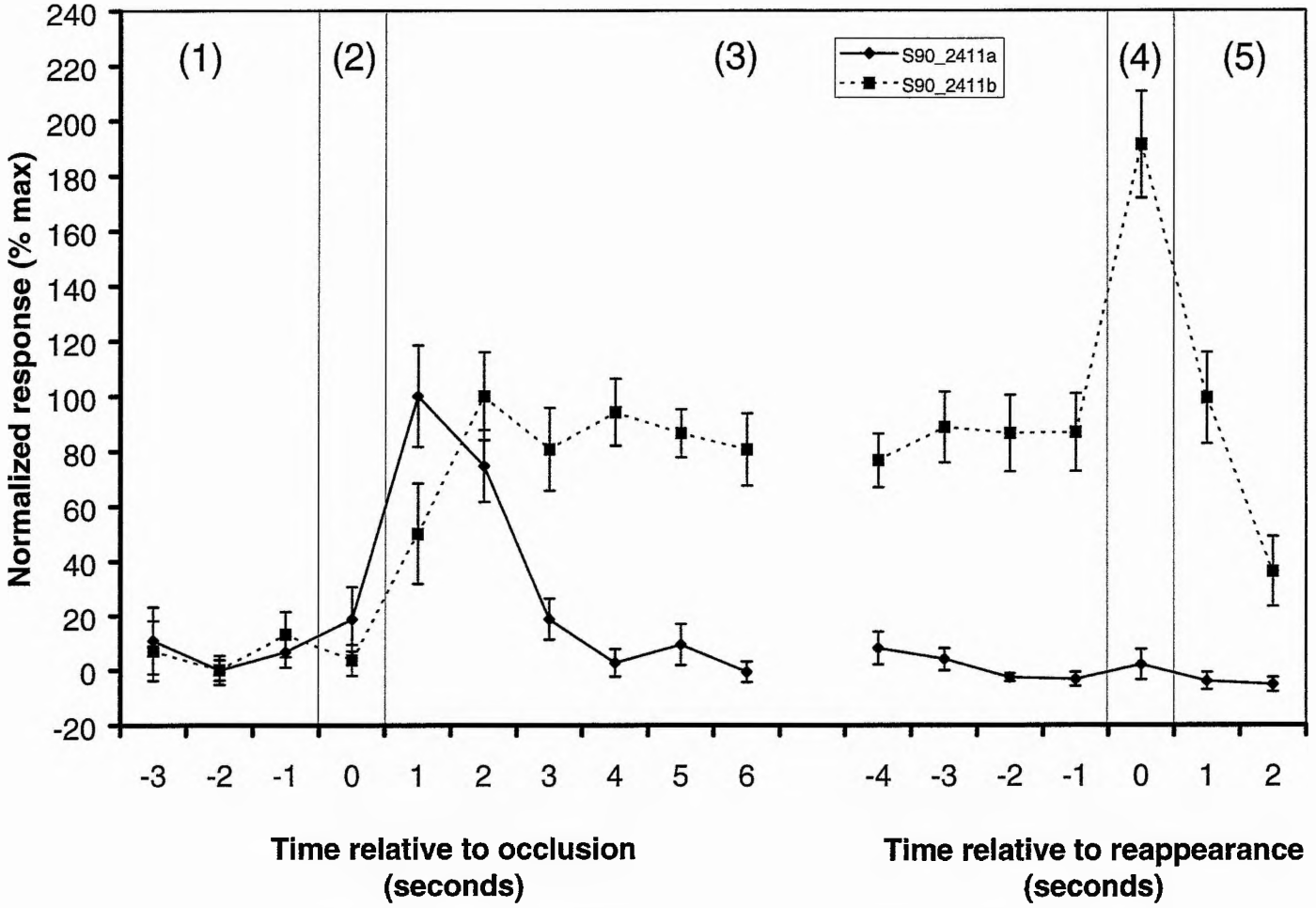


Figure 6.14 Responses of two simultaneously recorded neurons showing different patterns of activity throughout the different phases of the visual stimulus.Each cell, n=7.

6.3.5 Overall response profiles

(a) Occlusion and reappearance

The nature of responses at reappearance was not systematically related to the activity observed during the occlusion sequence. The range of different response patterns was evident even in neighbouring cells. For example, two simultaneously recorded neurones (Figure 6.14) exhibited different patterns of activity during both the occlusion and reappearance sequences. Cell S90_2411a showed a short duration increase in activity in the out of sight phase following occlusion of the experimenter with no change in activity during the reappearance sequence. By contrast, cell S90_2411b showed a longer latency to reach peak activity and more sustained levels of activity in the out of sight phase following occlusion of the experimenter. On reappearance there was a large, short duration increase in activity.

(b) Position, direction and overall responses

The effect of position and direction of movement on responses in the out of sight phase has already been described (see section 6.3.2c). Here I will describe in detail the results in terms of the overall response patterns, examining the effect of position and direction of movement on both the occlusion and reappearance sequences. For four cells sufficient data was collected on different positions of occlusion, with different directions of movement on both approach and reappearance, to enable this analysis. This analysis indicates additional levels of complexity in the responses of the cells described. These cells were tested on both

central and lateral occlusion. For two cells, both lateral positions (left and right) were tested and for the other two cells, one lateral position (right) only was tested. The cells were tested with a continuous sequence of movement and the data divided and aligned with the separate occlusion and reappearance phases.

Cell S97_2481a was tested with occlusion on the right side of the laboratory and centrally. There are three separate occlusion conditions as illustrated in figure 6.15. These occlusion conditions differ in terms of the position of the different phases and the directions of movement involved. The data for the occlusion sequence was analysed with a two-way repeated measures ANOVAs with time as a within-subjects factor and occlusion condition as a between-subjects factor. This analysis was repeated for the reappearance sequence.

For the occlusion sequence there is a main effect of both occlusion condition ($F_{2, 12} = 42.3$, $p<0.0001$) and time ($F_{4.0, 47.4} = 8.82$, $p<0.0001$) with a significant time by occlusion condition interaction ($F_{7.9, 47.4} = 4.0$, $p<0.002$). These results indicate that there was an overall change in activity over time, but that changes in activity were not equal for all three occlusion conditions.

For the reappearance sequence, there is a main effect of both occlusion condition ($F_{2, 11} = 8.3$, $p<0.01$) but no main effect of time ($F3.7, 41.0 = 0.51$, $p>0.05$). There is, however, a significant time by occlusion condition interaction ($F_{7.5, 41.0} = 4.1$, $p<0.002$). These results indicate differences in activity between the occlusion conditions, but no overall change in activity over time. The interaction shows that the changes in activity over time are not equal for the different occlusion conditions.

Breakdown of the results allows different comparisons to be made identifying the effects of position and direction of movement on the activity in the different phases of the stimulus.

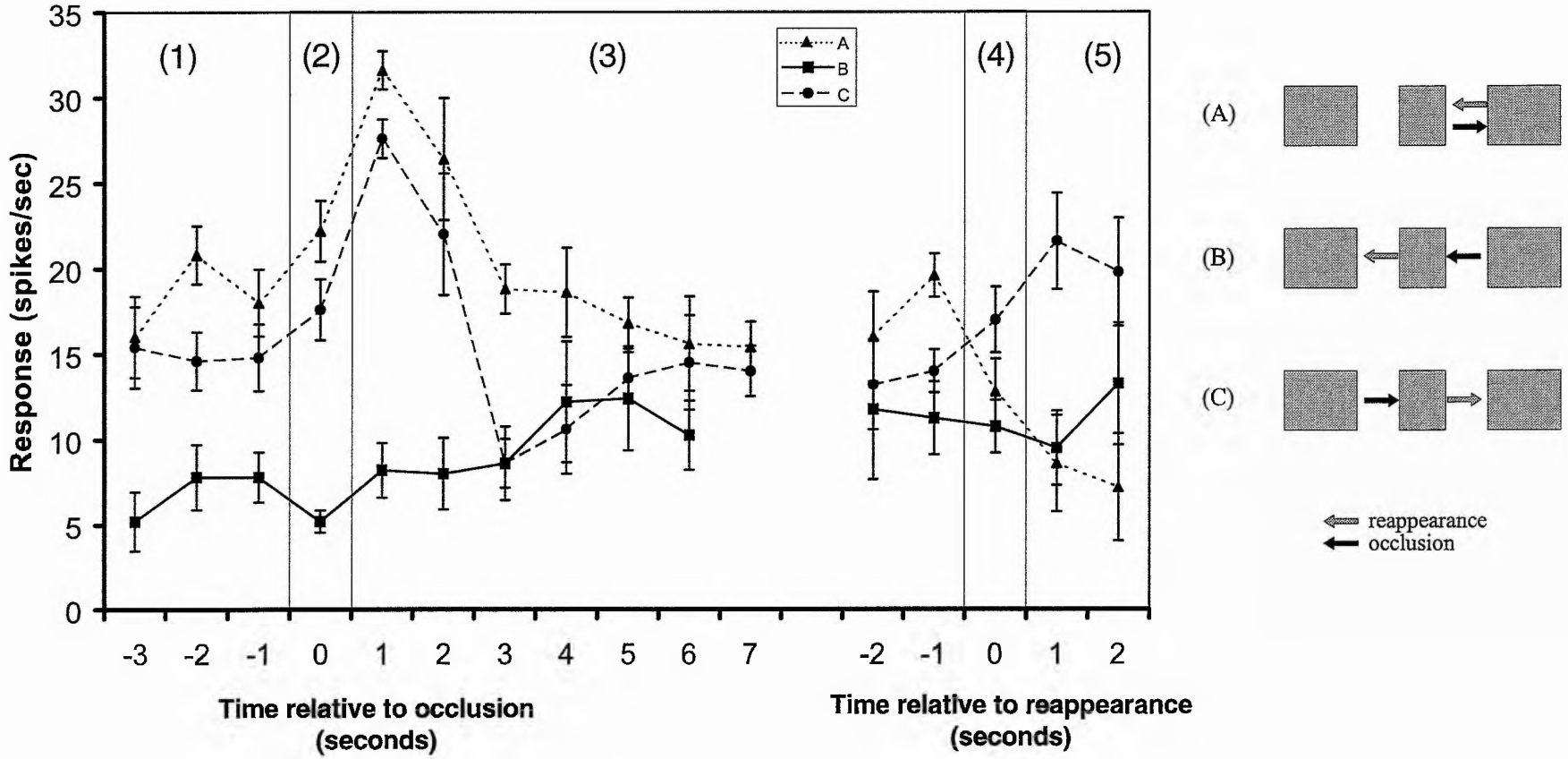


Figure 6.15 Responses of cell S97_2481a under three different occlusion conditions. The different testing conditions are illustrated on the right hand side of the figure. Each condition, n=5.

Two comparisons allow the influence of position and direction of movement on occlusion and out of sight phase responses to be analysed:

A1. A versus C. Direction of movement prior to occlusion is the same for these two conditions, but the position of occlusion differs.

A2. B versus C. The position of occlusion is the same but the direction of prior movement is different.

Comparison A1 - in both conditions there is a short duration increase in activity (C: -3 seconds pre-occlusion<1 second post-occlusion; A: -3<1, 2) following occlusion before levels drop to pre-occlusion levels. The only significant differences between the two conditions are in the out-of-sight phase (1 and 3 seconds post-occlusion) with greater levels of activity following occlusion on the right than in the centre. There are no significant differences in pre-occlusion activity.

Comparison A2 - with leftward movement there is no significant change in activity following occlusion. With rightward movement, however, there is a short increase in activity (-3<1) before levels drop to pre-occlusion levels.

These two comparisons demonstrate that there is an influence of *both position and direction of movement* prior to occlusion on the responses of the cell during the out-of-sight phase.

Two further comparisons allow the influence of position and direction of movement on reappearance phase responses to be analysed:

B1. A versus B. In these two conditions the direction of movement during reappearance is the same but the position of reappearance is different.

B2. A versus C. The direction of movement on reappearance differs but the position of movement coincides.

Comparison B1 - there is a decrease in activity on reappearance following occlusion on the right side of the lab (-1 seconds pre-reappearance>1, 2 seconds post-reappearance). No such change in activity is observed when the reappearance is from the central occluder with the same direction of movement.

Comparison B2 - there is a non-significant increase in activity with a rightward movement on reappearance, but a significant decrease in activity with a leftward movement to the same location (-1>1, 2). The only significant differences in activity between the two conditions occur following reappearance (1, 2) with greater activity for rightward than leftward movement.

These comparisons suggest that there is also an effect of *both position and direction of movement* on responses on reappearance.

There is a clear difference in the pre-occlusion levels of activity between conditions A and C, and B. A final two comparisons allow the effect of position and direction of movement on in-sight responses to be analysed.

C1. A versus C - direction of movement is the same but the position of movement differs.

C2. A versus B - the direction of movement differs but the position of the movement coincides.

Comparison C1 - there is no difference in the pre-occlusion activity in these two conditions.

Comparison C2 - pre-occlusion activity is greater in B than C throughout the pre-occlusion sequence.

These two comparisons suggest that for in-sight movement there is an effect of *direction of movement* with rightward being preferred to leftward, but *no effect of the position* of movement.

Overall, these results demonstrate that for the responses of this cell there is selectivity for position and direction of movement during many of the different stimulus phases. In the out of sight phase, greater responses are elicited following rightward than leftward movement, and a right-sided position elicits more activity than a central position. On reappearance, there is a drop in activity for leftward movement, but an increase in activity for rightward movement, and more inhibition for a right-sided position than a central position. For in-sight movement there is greater activity for rightward over leftward movement at a constant position. The results could be interpreted in a goal-orientated manner where the goal is a right-sided position. Any stimulus configuration that has a rightward component (in terms of direction of movement or position - i.e. move right, on the right) produces increases in activity whereas those stimulus configurations with a leftward component (move left, on the left) produce decreases or no change in activity or no change.

The following example shows different patterns of activity and different effects of position and direction of movement on pre-occlusion, out-of-sight and reappearance responses. For cell T8_2645, occlusion was tested on both sides of the laboratory and in the centre. The responses of this cell have been presented earlier in figure 6.8. The four different occlusion conditions used in testing and the results are shown in figure 6.16. Three of these conditions are the same as tested for the previous cell. For both the occlusion and reappearance sequences, data was analysed with two-way repeated measures ANOVA with time as a within-subjects factor and occlusion condition as a between subjects factor.

For the occlusion sequence there is a main effect of both time ($F_{3.5, 97.8} = 4.4$, $p<0.01$) and occlusion condition ($F_{3, 28} = 9.2$, $p<0.0003$) with a significant time by

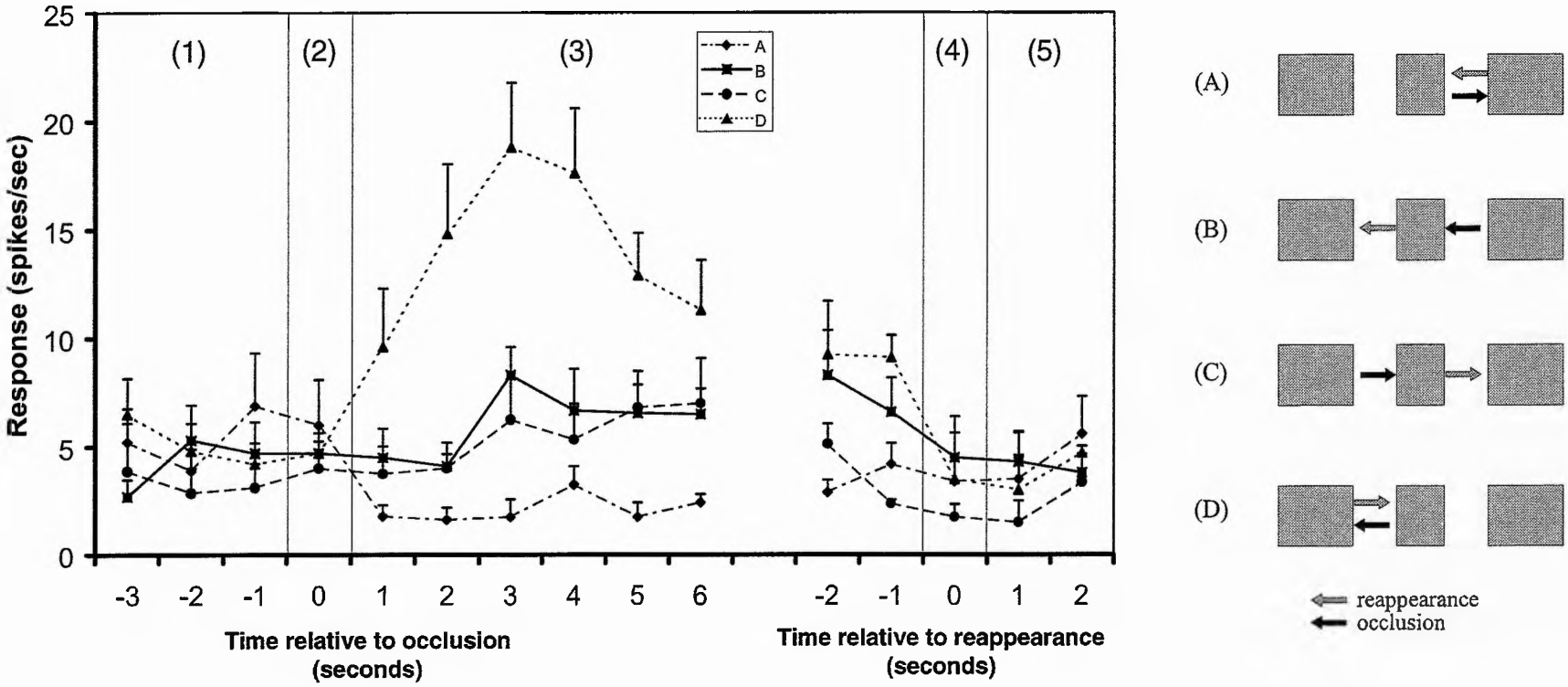


Figure 6.16 Responses of cell T8_2645a to four different occlusion conditions. The different testing conditions are illustrated on the right hand side of the figure. A, n=9; B, n=9; C, n=8; D, n=10.

occlusion condition interaction ($F_{10.5, 97.8} = 4.1$, $p<0.0001$). These results indicate that there was an overall change in activity over time, but that changes in activity were not equal for the four different occlusion conditions.

For the reappearance sequence there is a main effect of time ($F_{3.7, 107.5} = 2.7$, $p<0.05$), but no main effect of occlusion condition ($F_{3, 29} = 2.6$, $p>0.05$) and no significant interaction ($F_{11.1, 107.5} = 1.5$, $p>0.05$). These results indicate that there was an overall change in activity over time, but that there was no difference between the occlusion conditions.

Three comparisons allow the influence of position and direction of movement prior to occlusion on the responses during the occlusion and out of sight phases to be analysed.

A1. B versus D. In both these conditions, the direction of movement prior to occlusion is leftward, but the position of occlusion differs.

A2. A versus C. In both these conditions, the direction of movement prior to occlusion is rightward, but the position of occlusion differs.

A3. B versus C. The position of occlusion is the same in these two conditions but the direction of movement prior to occlusion is different.

Comparison A1 - in D there is an increase in activity during the out-of-sight phase (-3<2, 3, 4; -2=-1<2, 3, 4, 5), but there is no change in activity in B. There is no difference in pre-occlusion levels between the two conditions.

Comparison A2 - there are no significant differences between the two conditions, although there is slightly more activity in C than A during the out-of-sight phase.

Comparison A3 - in both conditions, there are no significant changes in activity over time, and no significant differences between the two conditions.

These comparisons show that for this cell there is an *effect of position but not of direction of movement* prior to occlusion on responses during the out-of-sight phase.

For reappearance, four similar comparisons allow the effect of position and direction of movement to be analysed.

B1. C versus D. Both conditions have rightward movement on reappearance but a different position of movement.

B2. A versus B. Both conditions have leftward movement on reappearance but a different position of movement.

B3. A versus C. Different directions of movement but the positions of reappearance coincide.

B4. B versus D. Different directions of movement but the positions of reappearance coincide.

As suggested by the results of the ANOVA, for all comparisons there are no significant changes in activity and no differences between the conditions. These results demonstrate that for reappearance there is *no effect of position or direction of movement* on responses during the reappearance sequence.

There are also no significant differences between the pre-occlusion activity in any of the conditions suggesting that there is *no effect of position or direction of movement* on activity elicited by in-sight movement.

In contrast to the previous cell, this cell shows differences in activity related to position, but not direction of movement, in the out-of-sight phase only.

The other two cells for which sufficient data was available showed similar patterns of activity as the two described in detail here with one having a pattern similar to T8_2645a and one similar to S97_2481a.

6.3.6 Eye movements

Observations of the eye movements both during testing and offline from the video recordings made during recording sessions showed that responses did not depend in any simple way on eye position. Selectivity between stimuli was found despite similar patterns of fixation and eye movements. Responses were observed both when the subject looked at the site of occlusion and when the subject was looking in other directions. Furthermore, fixation of the occluder did not produce responses in the absence of a hidden stimulus. Fixation was not necessary or sufficient to account for cell responses to stimuli out-of-sight. Simultaneously recorded neurones (identical eye movements and testing stimuli) were often found to exhibit different patterns of activity throughout the different phases of the stimulus (for example, see figure 6.12).

6.3.7 Cell localisation

The pattern of white and grey matter (quiet and cell zones, respectively) encountered during recording sessions was consistent with localisation within STS.

The x-ray reconstructions for each monkey are given in appendix B. The x-rays are consistent with those taken from previous monkey subjects in which the site of STS was confirmed histologically.

The location of the micro-lesion made at the end of the final recording session in Steve is shown in the histological section in appendix C. The lesion is clearly within the upper bank of STS. Visualisation of DiI confirmed this location.

Comparison of the x-ray of the final recording track with the site of the cells reported in this chapter shows the lesion to be at a similar depth and laterality to the cells but at a slightly more anterior location.

All this evidence demonstrates that the cells were recorded from within the banks of STSa. The bimodal nature of some of the cells and the evidence from histology suggests that the cells were located within the upper bank of the sulcus.

6.4 Discussion

6.4.1 Summary of results

The cells reported in this chapter showed:

(a) Increased levels of activity following occlusion of an object from sight compared with pre-occlusion levels.

(b) Changes in activity dependent on the site of occlusion within the laboratory. Such position sensitivity appears to be coded in an allocentric reference frame.

(c) Selectivity for form - observed in two thirds of the cells tested. In the majority of cases greater activity was observed following occlusion of the experimenter than other objects.

Responses may further be affected by the direction of movement, although it is important to realise that direction of movement and position are not mutually exclusive. For example, occlusion on the right side of the laboratory can only be preceded by rightward movement. Detailed analysis in some cells has revealed a complexity of responses that may be best described in goal-directed terms, in which the goal is a spatial position (see chapter 2).

By maintaining a position-selective representation of an object that has been occluded from sight these cells could contribute to object permanence.

6.4.2 Brain structures implicated in object permanence

The prefrontal cortex has been implicated in the performance of some object permanence tasks (Diamond and Goldman-Rakic, 1989). Monkeys with bilateral prefrontal cortex ablations exhibit similar patterns of performance and errors as 7.5-9 month-old infants on tests of the A not B error (Diamond and Goldman-Rakic, 1989; see chapter 3). Delay between the hiding of the object and retrieval is critically important (both prefrontally ablated monkeys and 7.5-9 month-old infants perform correctly with no delay). The poor performance could therefore be attributed to a memory deficit. Performance with a constant delay, however, is not comparable across different trial types. Errors are more frequent on trials with a change in hiding location following a correct response than on trials with a change in hiding location

following an incorrect response or trials with a repeated hiding location following either a correct or incorrect response. The poor performance of young infants and prefrontally ablated monkeys may be related to the inability to inhibit a prepotent response (Diamond, 1988; Diamond and Goldman-Rakic, 1989). Monkeys with hippocampal lesions also perform poorly on the A not B task, but only with delays greater than 15 seconds (Diamond *et al.*, 1989). Critically, these monkeys do not show the typical A not B error pattern with equal performance across all trial types suggesting that memory impairment alone cannot account for the A not B error and arguing against hippocampal involvement.

It is important to realise that the presence of the A not B error does not reflect lack of object permanence (see chapter 3). The studies described above suggest an involvement of the dorsolateral prefrontal cortex in the performance of the A not B task, but not in object permanence *per se*. The results described in the current chapter suggest that STSa may be involved in object permanence at a perceptual level.

6.4.3 Effect of eye movements

The effect of eye movements on the responses of the cells recorded was not extensively studied. Eye movement recordings were not made for all cells tested and the influence of eye movements on responses cannot be excluded. Observation of the eye movements during testing and from video records shows that the cell responses were not related to eye movement or position in any simple way. Selectivity between stimuli was observed despite similar patterns of eye movements and fixations. Responses during the out-of-sight phase were evident whether the monkey was fixating the site of occlusion or not. The simultaneous recording of neurones

provides examples of identical eye movements and identical stimulus conditions for different cells. In these cases the responses observed were often completely different (e.g. figure 6.12). The two cells illustrated showed a different pattern of activity in both the occlusion and reappearance sequences. It is unlikely that such a difference can be explained by recourse to eye movements.

Previous studies in both temporal (Yakovlev *et al.*, 1998; Nakamura and Kubota, 1995; Colombo and Graziano, 1994) and prefrontal cortex (O'Scalaidhe *et al.*, 1997) have found no effect of eye movements on responses occurring after stimulus presentation (equivalent to the out-of-sight phase of the current study). There are reports of eye movement related responses in posterior STS (Colby and Miller, 1986; Colby, 1991), but only a small proportion of cells (6%) showed exclusively eye movement related activity (see Oram and Perrett, 1994; Oram *et al.*, 1993 for discussion). Lesions of STP have been shown to produce temporary deficits in the productions of eye movements (Ó Scalaidhe *et al.*, 1995, 1997), although the lesions included most of the length of STP. As described in chapter 2, the cell properties are heterogeneous along the length of the sulcus and the eye movement deficits may result primarily from damage to posterior regions. The current cells were recorded in anterior regions of STS, close to the temporal pole, where you would expect fewer eye movement related responses than in more posterior parts of the same sulcus (Oram *et al.*, 1993). Indeed, in previous studies of cells in STSa, no effect has been found of eye movements on responses to static and motion stimuli (e.g. Perrett *et al.*, 1991a; Oram *et al.*, 1992, 1993)

6.4.4 Responses in the absence of stimuli

Stimulus selective neuronal responses occurring after stimulus presentation have been reported in temporal (Fuster, 1990; Baylis and Rolls, 1987; Mikami, 1995; Fuster and Jervey, 1982; Colombo and Gross, 1994; Desimone, 1996), parietal (Koch and Fuster, 1989), auditory (Gottlieb *et al.*, 1989) and prefrontal cortex (Fuster and Alexander, 1971; Kubota and Niki, 1971; Funahashi *et al.*, 1989; Miller *et al.*, 1996). Typically this activity occurs in structured tasks in which the stimuli must be remembered to guide subsequent behavioural responses. Modulation of cell activity during the interval between stimuli ("delay-activity") in delayed matching to sample tasks has been attributed to the explicit training of subjects and the mnemonic requirement of the task (Fuster, 1973; Desimone *et al.*, 1995). The delay activity is not observed in untrained animals or in trained animals during control tasks in which memory is not required (Fuster, 1973; Desimone *et al.*, 1995), and its magnitude may reflect task difficulty (Gibson and Maunsell, 1997). In prefrontal cortex it has been suggested that the responses of neurones may be tuned to the behavioural demands (Rao *et al.*, 1997) and this may account for the different patterns of delay activity observed in different studies.

The activity of the population of cells reported here occurs in the absence of any experimental task. Indeed, neither of the two subjects had been trained in any mnemonic task requiring memory for stimulus attributes. The test situation makes no behavioural demands but the existence of cells with responses during natural occlusion may reflect the everyday experience of objects being temporarily occluded from sight and subsequently reappearing.

Activity in prefrontal cortex continuing or beginning following the offset of facial stimuli in tasks in which there was no mnemonic requirement has been reported (O'Scalaidhe *et al.*, 1997). Two out of three monkeys, however, had previously been trained on mnemonic retention tasks with similar visual stimuli and only 6 cells were reported with activity selective for the period following offset of the visual stimulus.

6.4.5 Importance of gradual occlusion

Phenomenological studies have shown that gradual occlusion (see figure 3.4) is one of the principal cues for object permanence in humans (Michotte, 1950; Gibson, 1979; Gibson *et al.*, 1969; see chapter 3). Gradual occlusion was inherent in the stimuli used in the experiments described in this chapter. The test situation examined here is very different to that of Assad and Maunsell (1995) who measured parietal cell activity to inferred motion during the temporary disappearance of a moving dot. In individual trials of their task there was no intrinsic information at the moment of disappearance from which to infer motion or continued existence.

The shutter test used here was designed to determine if the cells were responding simply to the disappearance of a visual stimulus from view or if the manner of disappearance was important. Specifically the test compared responses to disappearance through gradual occlusion (as in the rest of the testing) to disappearance through the closure of a shutter. The majority of cells (80%) gave differential responses between the gradual occlusion and shutter conditions. This is suggestive of the importance of gradual occlusion in eliciting cell activity. There are, however several other differences between the two conditions. In the occlusion

condition the experimenter is moving whereas in the shutter condition the experimenter is static. If movement is critical for the cells to respond this could account for the lack of response in the shutter condition. After the experimenter has moved out of sight in the occlusion condition the room is still visible whereas in the shutter condition all visual stimulation is removed. When the shutter closes it is not just the experimenter that disappears from view, but all visual stimuli.

6.4.6 Selectivity for object form

The vast majority of the cells showing form sensitivity were selective for the experimenter over other objects (e.g. mobile chair, television stand). In the normal "home-cage" environment and in the laboratory, objects involved in occlusion would generally be self-propelled conspecifics or humans. Inanimate objects would rarely be occluded except through the movements of the subject. Cotton-top tamarins have recently been shown to be aware of the animate/inanimate distinction in generating expectations about object movement (Hauser, 1998; Hauser and Carey, 1998; see chapter 4). Human infants may show person permanence before a more general object permanence (e.g. Bell, 1970; Legerstee, 1994) and this may reflect the social context of the situation (Legerstee, 1994). It has been suggested (Dumas and Brunet, 1994) that non-human primates failure on invisible displacement tasks may be due to the use of inanimate objects in the testing. Primates may have a propensity for dealing with problems with a social content (see Anderson, 1998).

6.4.7 Temporal cortex and space

The spatial sensitivity exhibited by the cells described here has not been reported previously in temporal neocortex. Lesion studies have led to the distinction between dorsal and ventral streams of cortical visual processing responsible for analysis of object position and analysis of object form respectively (e.g. Ungerleider and Mishkin, 1982; see chapter 2). An alternative dichotomy, however, based on the outputs of the systems suggests that position and form may be coded in both streams but for different functions: visuomotor behavior and object/scene recognition (Milner and Goodale, 1995). The spatial sensitivity in temporal cortex reported here fits more with the latter functional distinction.

Anatomical studies have shown that STSa is a site of reconvergence of the dorsal and ventral streams, the area receiving inputs from inferior temporal and parietal cortex and from posterior motion processing regions (e.g. Boussaoud *et al.*, 1990; Baizer *et al.*, 1991; see chapter 2). Such anatomical evidence predicts STSa to be a site of integration of object and spatial information. The current data are the first evidence supporting this prediction. The spatial sensitivity, however, could arise from many different areas including parietal and parahippocampal cortex or could be derived from processing in early stages of the ventral stream (see chapter 8).

The ability to search successfully for an object hidden from sight relies on awareness of both the object's continued existence and its likely location. By maintaining a position-selective representation of an object that has been occluded from sight the cells described here could provide a neural basis for object permanence.

6.5 SUMMARY

The cells reported in this chapter showed increased activity following the occlusion of a visual stimulus compared with pre-occlusion levels. All cells showed selectivity for the location of occlusion within the room and this position sensitivity may be coded in an allocentric manner. Responses may further be affected by the direction of movement during the different phases of the stimulus. Such position selectivity has not previously been reported in temporal neocortex and fits with predictions from anatomy suggesting integration of object and spatial information in anterior regions of STSa. The manner of disappearance was found to be critical with the majority of cells tested not responding to sudden disappearance of a visual stimulus without gradual occlusion.

CHAPTER 7

AUDITORY-VISUAL INTERACTIONS

7.1 INTRODUCTION

7.1.1 The problem of multimodal perception

In the natural environment, objects are perceived across different modalities. An object that stimulates tactually can also be perceived visually and any sounds that the object makes will be perceived through the auditory modality. To be able to relate different perceptions across modalities requires some degree of "binding" or cross-modal integration. For example, to identify visually the source of a given sound requires the visual and auditory information to be "matched". In cluttered environments where there are numerous sounds and objects such cross-modal matching becomes a demanding process.

Piaget (1952, 1954) assumed that the different modalities were separate at birth and that during development there was a gradual co-ordination of the sensory modalities (see also Meltzoff, 1981). Similar to his views on object permanence (see chapter 3), he saw this co-ordination arising through exploration of the physical environment. An object might be manipulated tactually, allowing correlation with the simultaneous visual perception. This view has been challenged by evidence that cross-modal matching appears very early in infancy (e.g. Meltzoff and Borton, 1979; Kuhl and Meltzoff, 1982; Gibson and Walker, 1984; Streri, 1987). For example, Meltzoff and Borton (1979) reported that 29-day old infants are capable of

discriminating which of two visually presented objects they had previously explored tactually in their mouths. Infants of this age are too young to have watched themselves handling different objects and such evidence suggests that intermodal co-ordination may be an innate ability (Meltzoff, 1981).

Kuhl and Meltzoff (1982) presented 18 to 20 week old infants with a film showing two identical heads mouthing different vowel sounds. A soundtrack played to the infants simultaneously (synchronized with the mouth movements) consisted of vowel sounds matching the articulations of one of the heads. The infants were found to look significantly longer at the head with articulations that matched the vowel sounds, suggesting that they are able to detect the cross-modal relationship between the visual articulations and the sounds.

There are numerous cues available for the binding of different modality stimuli, many related to the Gestalt principles of object perception (Radeau, 1994). The most significant of these are: (a) Proximity – different stimuli arising from the same location in space are likely to be related; (b) Temporal correlation – stimuli occurring at the same time and with the same temporal pattern are likely to belong together; and (c) acquired knowledge – for example, knowledge of sex differences suggests that a deep voice is more likely to be coming from a man than a woman, from an adult rather than a child.

7.1.1 Examples of polysensory interactions

At a behavioural level, a good example of interactions between visual and auditory stimuli is the McGurk effect (;McGurk and MacDonald, 1976; MacDonald and McGurk, 1978) relating to the perception of speech sounds. If the visual

information (lip movements) for the sound /ga/ is associated with the auditorily presented /ba/, human subjects often report hearing /da/. Discordant visual and auditory information produces novel perceptions suggesting an interaction between visual and auditory information in perceiving speech. Evidence for the McGurk effect has been found even in pre-verbal infants as young as 5-months old (Rosenblum *et al.*, 1997). The interaction has also been demonstrated on a physiological level in the magnetoencephalographic waveforms recorded over the left temporal lobe (Sams *et al.*, 1991). The sight of visual articulation alone produces no response in the left temporal area, but the same visual articulation can modify the waveforms observed to auditorily presented syllables, suggesting that the visual information modifies responses in auditory cortex.

At the cellular level, inputs from the different sensory systems are found to converge on individual neurones (multi- or poly-sensory neurones) in many different brain areas in the macaque (e.g. STS: Bruce *et al.*, 1981; superior colliculus: Wallace *et al.*, 1996; ventral premotor cortex: e.g. Graziano *et al.*, 1997b: orbitofrontal cortex: Rolls and Baylis, 1994; ventral intraparietal area, VIP: Duhamel *et al.*, 1991). Such convergence may provide the basis for cross-modal matching.

The superior colliculus is involved in the localisation of sensory stimuli and in directing gaze and attention towards stimuli (see Knudsen and Brainard, 1995 for recent review). Multisensory integration within this structure provides a good example of the interactions that may occur at a cellular level. The properties of cells within the superior colliculus are generally consistent across species (Knudsen and Brainard, 1995), but here I will focus on studies in the primate. Two of the cues described above for binding auditory and visual stimuli (common spatial position and common timing) seem to play a role in the superior colliculus. In individual

polysensory neurones, the receptive fields (RFs) for different modalities are found to coincide (e.g. Wallace and Stein, 1996) and the responses to one modality may be altered by the presence of a stimulus from a second modality (e.g. Wallace *et al.*, 1996). These cells often exhibit non-linear summation to simultaneously presented auditory, visual and somatosensory stimuli. For example, if an auditory and visual stimulus are both presented in the receptive fields of a given polysensory neurone, the observed response may be much greater than the responses to the auditory or visual stimulus alone, greater than the response that would be predicted by mere summation of responses (e.g. Wallace *et al.*, 1996). Multiple stimuli of one modality generally do not produce the same effect. These are similar to findings in the cat superior colliculus (e.g. Meredith and Stein, 1986a, b; Wallace *et al.*, 1998). If, however, one stimulus is presented within the receptive field and one is presented outside the receptive field, response depression may be observed (Wallace *et al.*, 1996). This suppressive effect was commonly observed with auditory stimuli inhibiting responses to visual and somatosensory stimuli, but the reverse was rarely observed.

In terms of timing, the degree of response enhancement or depression varies with the temporal disparity between the stimuli (Meredith *et al.*, 1987; Wallace *et al.*, 1996). For example, Wallace *et al.*, (1996) found that maximum interaction effects were observed for simultaneously presented polysensory stimuli presented less than 500ms apart (range 100-500ms).

Multisensory cells are also found in the ventral premotor cortex (F4) of macaques (e.g. Fogassi *et al.*, 1996; Graziano *et al.*, 1997b). Matching of different modality RFs similar to that seen in the superior colliculus is also found in this brain area, enabling cross-modal matching based on common position or proximity. For

example, in bimodal visual-tactile cells the visual RFs are found to extend outwards from the tactile receptive fields (Fogassi *et al.*, 1996). Furthermore, the visual receptive fields are tied to the tactile receptive fields, so that when, for example, the arm moves the receptive field moves correspondingly (Graziano *et al.*, 1994; see chapter 2).

7.1.2 Polysensory interactions in STS

There has been very little work on polysensory interactions in STS despite the extensive anatomical evidence for sensory convergence (e.g. Baizer *et al.*, 1991; Seltzer and Pandya, 1994) and numerous neurophysiological reports of polysensory activity (e.g. Bruce *et al.*, 1981; Hikosaka *et al.*, 1988; Mistlin and Perrett, 1990) in the upper bank of the sulcus (STP).

Desimone and Gross (1979) labelled the upper bank of STS, the superior temporal polysensory area (or STP; see chapter 2) on the basis of polysensory responses, but did not investigate cross-modal interactions. They presented independent visual, somatosensory and auditory stimuli but never simultaneously. In the caudal part of STS, adjacent to area MST, Hikosaka *et al.* (1988) reported bimodal neurones with congruent properties in both the visual and auditory modality in anaesthetised macaques. For example, auditory-visual cells responsive to movement were found to have similar selectivity for stimulus velocity in each modality. Similarly, some somatosensory-visual cells were found to have equivalent selectivity for direction of motion in each modality, responding to, for example, upward tactile movements and the sight of upward movements. Equivalent

somatosensory-visual congruence has been reported in ventral intraparietal area (Duhamel *et al.*, 1991).

As in other studies, Hikosaka *et al.* (1988) tested the different modalities independently and separately and no complex interactions were observed. Unlike the superior colliculus, the RFs for the different modalities of a single neurone did not always correspond. In many cases the RFs for the different modalities were complementary (i.e. spatially adjacent), but showed very little overlap.

Interaction between independent stimuli in STS was reported by Benevento *et al.* (1977) who found in the anaesthetised macaque that auditory stimuli often suppressed responses to visual stimuli. The auditory and visual stimuli, however, were never related and were often simple in nature e.g. bars and clicks.

Complex multimodal interactions have been reported when cells were tested with related stimuli. For example, Bruce, Desimone and Gross (1981) found a small number of cells that responded to an object striking a surface, but not to the sight or sound of the event alone. Both sight and sound of the event were required to elicit a response. In the tactile domain Mistlin and Perrett (1990) reported that bimodal (visual and tactile) neurones responded to related visual and tactile stimuli. Bimodal neurones with an "OFF" tactile response were found to respond to visual movement away from the body, whereas neurones with an "ON" tactile response also responded to visual movement towards the body (cells with similar properties have been reported in ventral intraparietal area - Duhamel, Colby and Goldberg, 1998). Mistlin and Perrett (1990) also found that tactile responses were often attenuated if the monkey could see the approach of the object towards the body. Such effects were discussed in terms of expectation with the suggestion that responses to "expected" stimuli are attenuated.

This chapter describes an investigation of cells with bimodal, auditory-visual responses. In particular the cells were tested for any evidence of multisensory interactions. For the cells with responses during visual occlusion, described in the previous chapter, it was noted that some were auditorily responsive but only when the experimenter was out of sight. The responses of the cells described in the current chapter were tested with the experimenter in- and out-of-sight, but for this group of cells there were no responses to the occlusion of visual stimuli as described for the cells in chapter 6. It was hypothesised that the auditory responses might be dependent on the concurrent visual stimulation.

7.2 Methods

Cells were tested clinically as described in the general experimental methods. Any cells that gave evidence of auditory responses were tested further. Cells were tested with a variety of different, briefly presented sounds (mostly experimenter produced - e.g. tapping feet, rustling curtains, clapping, imitating monkey calls, computer generated tone). Auditory responses were tested both when the experimenter was in-sight and when the experimenter was out-of-sight behind an occluder at different locations around the laboratory. The experimenter was static during testing apart from the movements required to produce the sounds (e.g. tapping of foot), and was either completely in-sight or completely out-of-sight for the duration of the sounds. Responses to the visually stimuli alone (experimenter in-sight or out-of-sight) were tested by making the same movements as in the sound conditions, but without the sound. Cell responses were recorded for 0.5 or 1.0 seconds following the production of the sound or appropriate movements. Responses

were analysed using one and two-way ANOVAs as appropriate with Tukey HSD post-hoc testing with $p < 0.05$ level of significance.

7.3 Results

7.3.1 General results

Out of 463 cells recorded in the anterior superior temporal sulcus, 60 had auditory responses and of these 15 cells showed differential responses to auditory stimuli when the experimenter was in- or out-of-sight. Seven of these cells also showed increasing levels of activity as the experimenter moved out of sight and were reported in the previous chapter. Here I will focus on the remaining 8 cells that all showed a predominant auditory response with no change in activity as objects were occluded. Four cells gave a greater response to auditory stimuli when the experimenter was in view and the remaining four cells gave a greater response when the experimenter was occluded from sight.

The cells showed broad selectivity for the nature of sounds. For example, cell T26_2863, responded to both the sound of jangling keys and knocking against a wall, but did not respond to imitation monkey calls, speech sounds or clapping. Similarly, cell T32_2801 responded to any tapping noises (e.g. foot on floor, metal on metal, metal on wood, wood on wood), but did not respond to clapping, rustling of curtains or imitation monkey calls. Sounds selected for testing were those that produced a consistent response from the cell and were easily reproducible.

The cell illustrated in figure 7.1 gave a significantly greater response to a sound (light tapping of the foot) when the experimenter was in view than when the

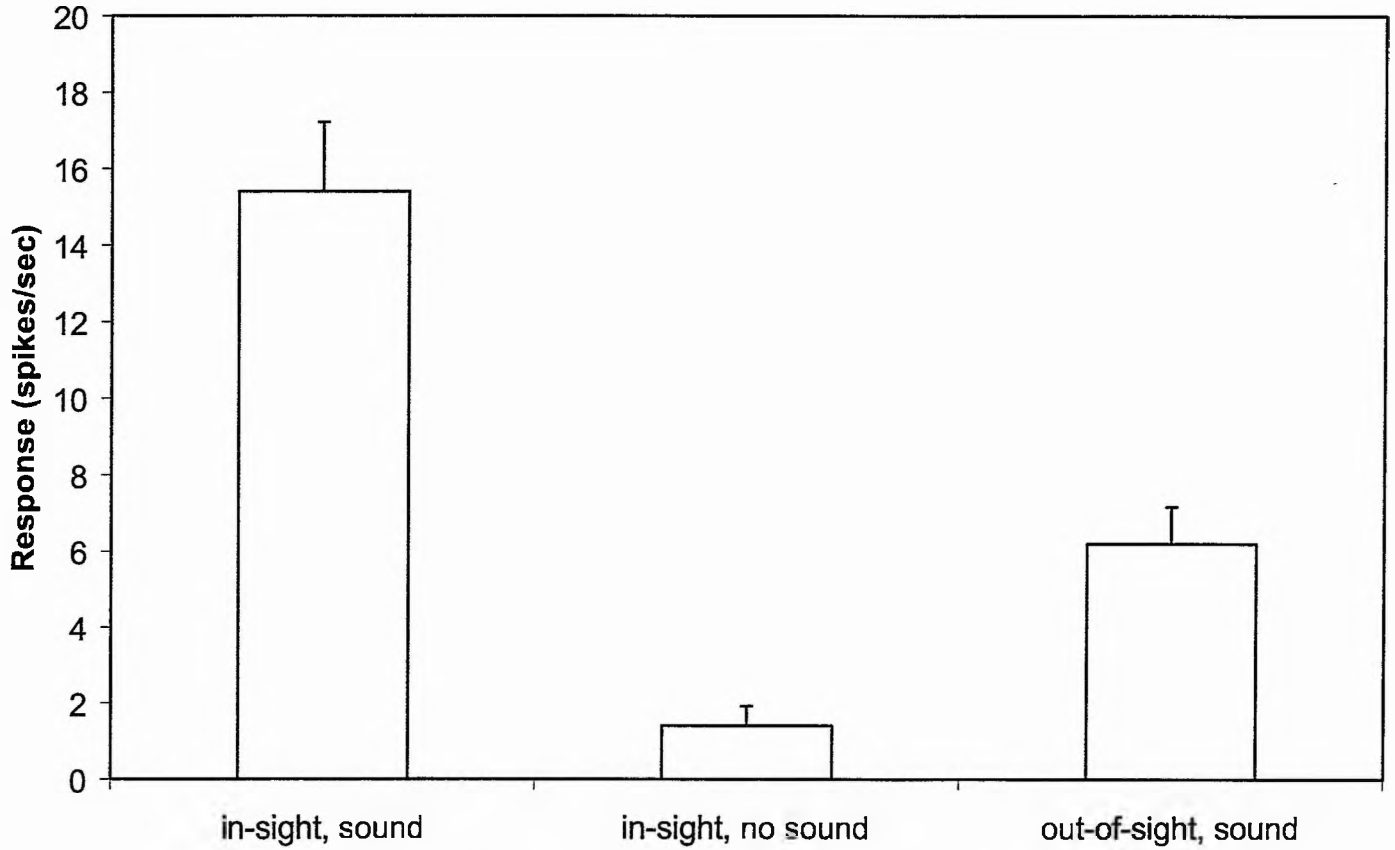


Figure 7.1 Responses of cell T12_3068 to sound produced by the experimenter in- and out-of-sight.The sound was light tapping of the foot, and responses are based on cell activity recorded for 0.5 seconds after production of the sound. One way ANOVA shows a significant effect of condition ($F_{2, 27} = 33.79$, $p < 0.0001$). Post-hoc testing shows that there is a greater response to in-sight noise than out-of-sight noise. This is not simply a visual response since there is little response to the experimenter in-sight with no sound (in-sight, no sound < other conditions). Each condition, n=10.

experimenter was occluded (sound, in-sight > sound, out-of-sight). In this case the occluder was the shutter box described in the general experimental methods. In-sight responses without sound were tested with the same movements as in the sound condition, but without contact being made between the foot and the ground. When the experimenter was out of sight the cell still showed a significant response to the sound (sound, out-of-sight > no sound, in-sight), but the response was attenuated relative to the sound, in-sight condition. The visual stimulus of the experimenter could be said to "enhance" the auditory response. The response to an auditory stimulus was greater when there was a concurrent visual stimulus than when the auditory stimulus was presented alone. Clinically, the cell showed similar baseline levels of activity when the experimenter was either in or out-of-sight and making no sound.

For this cell, it is interesting to note that the monkey could see the upper torso of the experimenter only and could not see the movement that was producing the sound. The experimenter was clearly in view, but the bottom of the legs was out-of-sight. A slight movement of the foot only was required to produce the sound and this was not visible to the monkey. Thus, sight of a stimulus associated with the production of the sound, but not sight of the actual sound production was sufficient to produce the cross-modal interaction.

In contrast, the cells illustrated in figures 7.2, 7.3 and 7.4 all showed the opposite effect: a greater response to auditory stimulation when the experimenter was out-of-sight. These cells were tested under four conditions in which the visibility of the experimenter (in- or out-of-sight) and sound production (sound or no-sound) were varied. The resulting 4 test conditions are summarised in table 7.1. The cells were analysed with two-way ANOVAs with visibility of experimenter and sound

Experimenter	Sound production
In-sight	Sound
In-sight	No-sound
Out-of-sight	Sound
Out-of-sight	No-sound

Table 7.1 Summary of the testing conditions for the cells illustrated in figures 7.2, 7.3, 7.4. The experimenter was in- or out-of-sight and either made a sound or was silent.

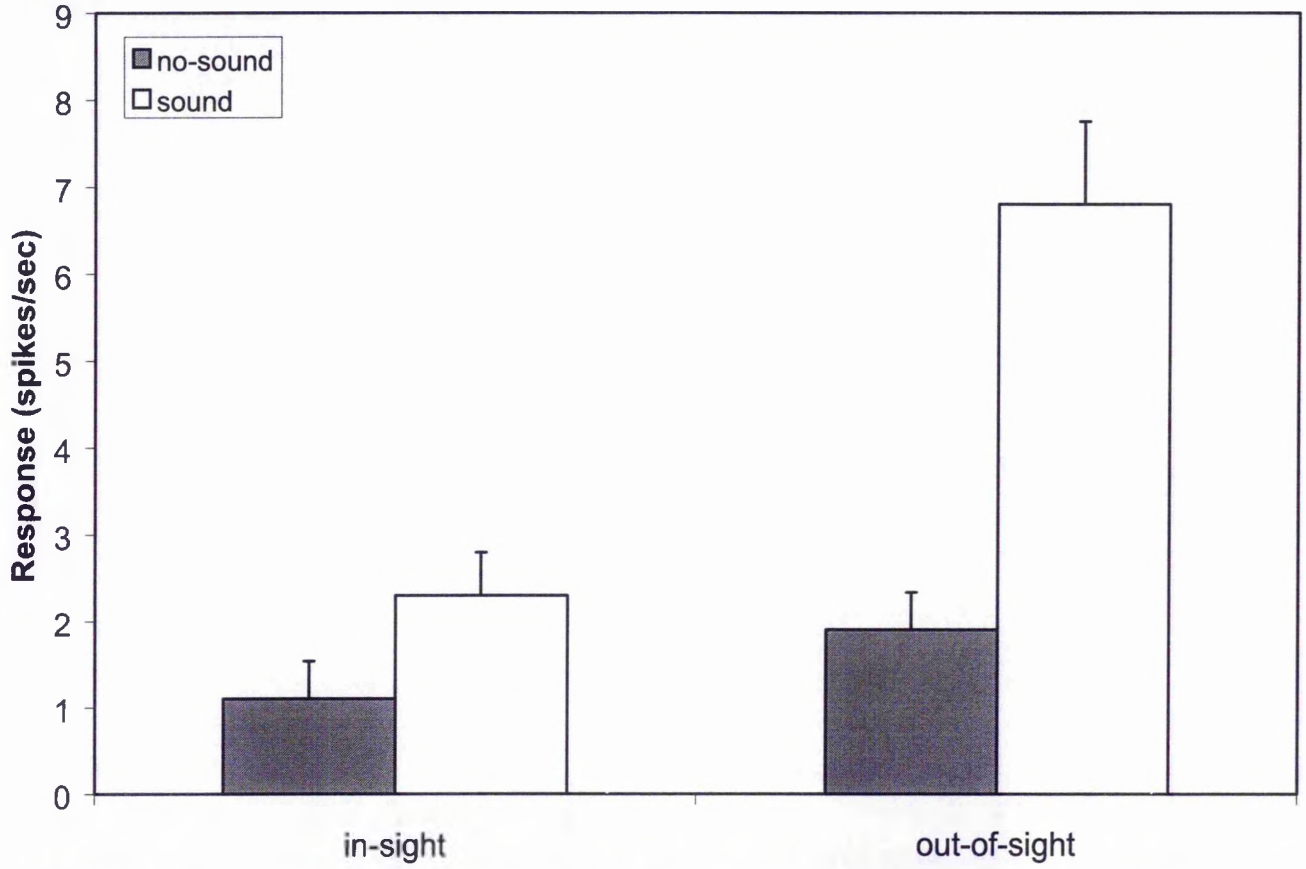


Figure 7.2 Responses of cell T26_2863 to sounds produced by the experimenter in- and out-of-sight. The sound was patting of the hand against the leg and responses are based on cell activity recorded for 1 second after production of the sound. Two-way ANOVA with sound and experimenter visibility as factors shows a main effect of both sound ($F_{1, 36} = 24.36$, $p < 0.00002$) and experimenter visibility ($F_{1, 36} = 18.39$, $p < 0.0002$) with a significant sound by visibility interaction ($F_{1, 36} = 8.96$, $p < 0.005$). Post-hoc testing shows the only significant differences to be between out-of-sight, sound and all of the other conditions. Each condition, n=10.

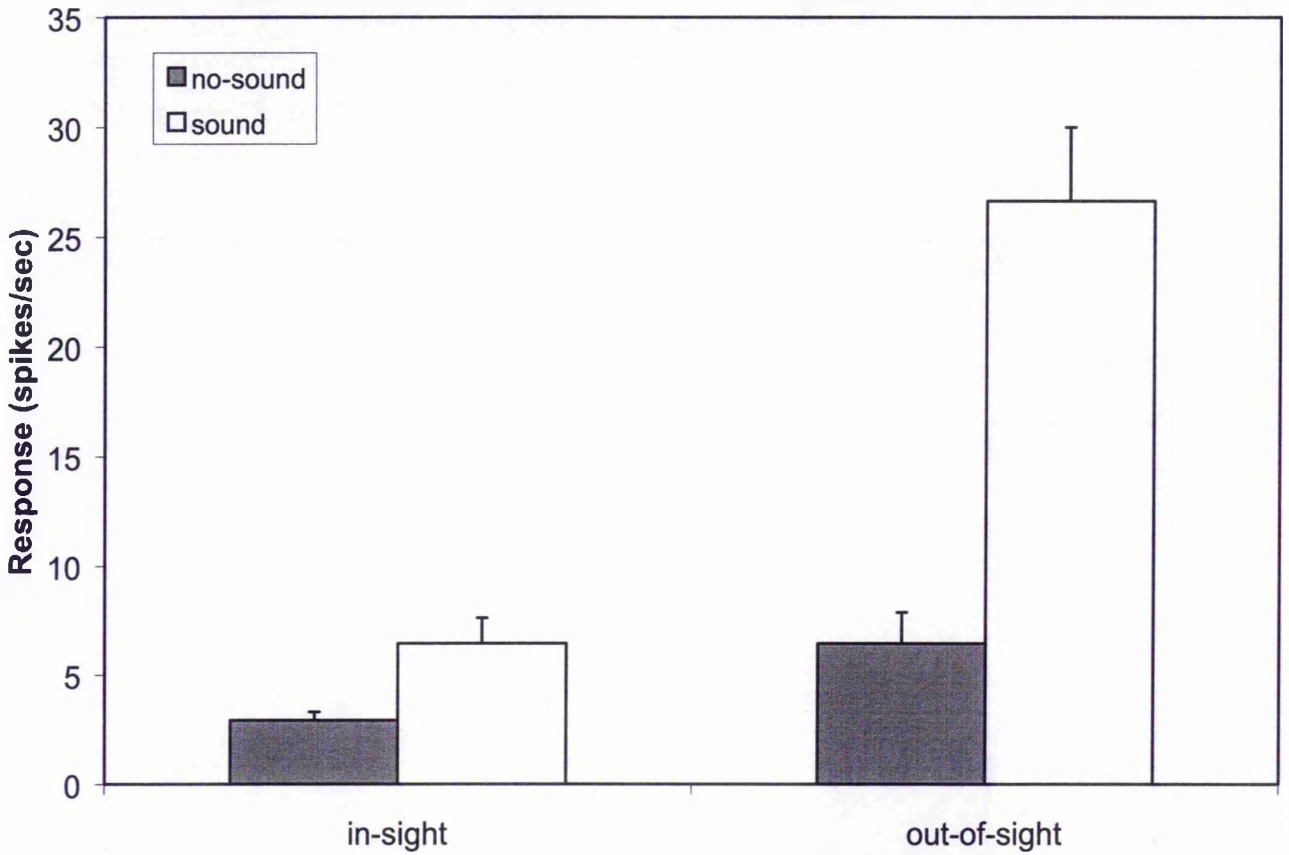


Figure 7.3 Responses of cell T28_3012 to sounds produced by the experimenter in- and out-of-sight. Sound was tapping of the foot and responses are based on cell activity recorded for 1 second after production of the sound. Two-way ANOVA with sound and experimenter visibility as factors shows a main effect of both sound ($F_{1, 40} = 41.71$, $p < 0.00001$) and experimenter visibility ($F_{1, 40} = 41.71$, $p < 0.00001$) with a significant sound by visibility interaction ($F_{1, 40} = 20.50$, $p < 0.0001$). Post-hoc testing shows the only significant differences to be between out-of-sight, sound and all of the other conditions. Each condition, n=11.

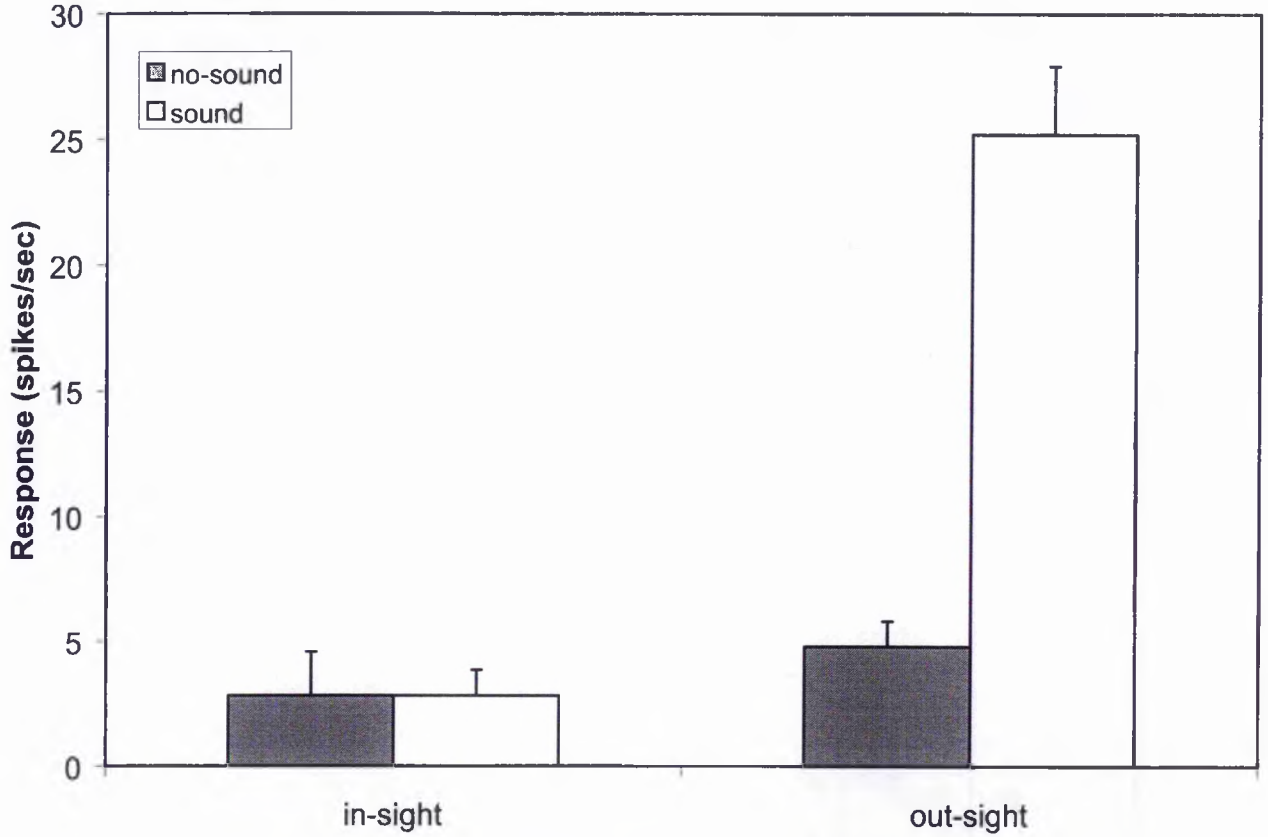


Figure 7.4 Responses of cell T32_2801a to sounds produced by the experimenter in- and out-of-sight. Sound was tapping of the foot and responses are based on cell activity recorded for 0.5 seconds after production of the sound. Two-way ANOVA with sound and experimenter visibility as factors shows a main effect of both sound ($F_{1, 16} = 33.13$, $p < 0.00001$) and experimenter visibility ($F_{1, 16} = 47.4$, $p < 0.00003$) with a significant sound by visibility interaction ($F_{1, 16} = 33.13$, $p < 0.00001$). Post-hoc testing shows the only significant difference to be between out-of-sight, sound and all of the other conditions. Each condition, n=5.

production as factors. The results for all three cells are qualitatively similar. In each analysis there is a significant main effect of experimenter visibility, a significant main effect of sound production and a significant experimenter visibility by sound production interaction (see figure legends for quantitative details of analyses). These analyses show that responses with the experimenter out-of-sight are greater than responses with the experimenter in-sight, that responses are greater when a sound is produced than when the experimenter is silent and that the effect of sound is greater in the out-of-sight than in the in-sight condition. This statistical interaction shows that the auditory-visual interaction is non-linear. It is clear from the results that the cells are not simply showing a summation of auditory and visual responses. For these cells, it seems as if the visual stimulus is "gating" an auditory response. In all 3 cells, the response when the experimenter is out-of-sight with no sound is greater than when in-sight with no sound, but in all cases this does not represent a significant difference. If there were a significant difference it would suggest a response during the occlusion of visual stimuli similar to that reported for the cells in the previous chapter.

7.3.2 Specificity of effects

In all the tests described so far, the sound and the visual stimulus were always in the same location, and the visual stimulus was the object (experimenter) producing the sound. In 3/4 cells described, the movements producing the sound were visible in the in-sight condition. The observed effects could be due to a general visual gating/enhancing of auditory responses by any visual object or there could be specificity for the nature of the object. To determine if the visual gating is specific to

particular visual objects or stimuli, two cells were tested with different visual stimuli in view. For this testing, the sound source was spatially separated from the experimenter. The sound source was either in or out-of-sight (with the corresponding movements producing the sound either in or out-of-sight) and the experimenter was either in or out-of-sight. The resulting four conditions of testing are summarised in table 7.2. The sounds were produced indirectly by the experimenter and could be produced in-sight without any part of the experimenter remaining visible. In one cell, the sound was produced by tapping a mop on a chair (T28_3012), and in the other cell, the sound was the rustling of curtains (T25_2961). Both cells were analysed with two-way ANOVAs with experimenter visibility and sound source visibility as factors.

The responses of cell T28_3012 (figure 7.5) show a main effect of both sound source visibility and experimenter visibility. Responses were greater when the sound was produced out-of-sight than when the sound was produced in-sight with the movements producing the sound visible. Responses were also greater when the experimenter was out-of-sight than when the experimenter was in-sight. This cell, therefore, showed attenuation of the response when either the experimenter or the sound source (mop and chair) was in-sight, although the effect of the visibility of the sound source was much greater than the effect of the experimenter. This suggests that the sound source with the corresponding movements producing the sound is the most effective visual stimulus in attenuating the auditory response.

A slightly different pattern of results is seen in the responses of cell T25_2961 (figure 7.6). Two-way ANOVA shows that there is a main effect of sound source visibility but no effect of experimenter visibility and no sound by experimenter interaction. Responses were greater when the sound source (curtains

Experimenter	Sound source
In-sight	In-sight
In-sight	Out-of-sight
Out-of-sight	In-sight
Out-of-sight	Out-of-sight

Table 7.2 Summary of the testing conditions for the cells illustrated in figures 7.5 and 7.6. The experimenter and the sound source were either in- or out-of-sight.

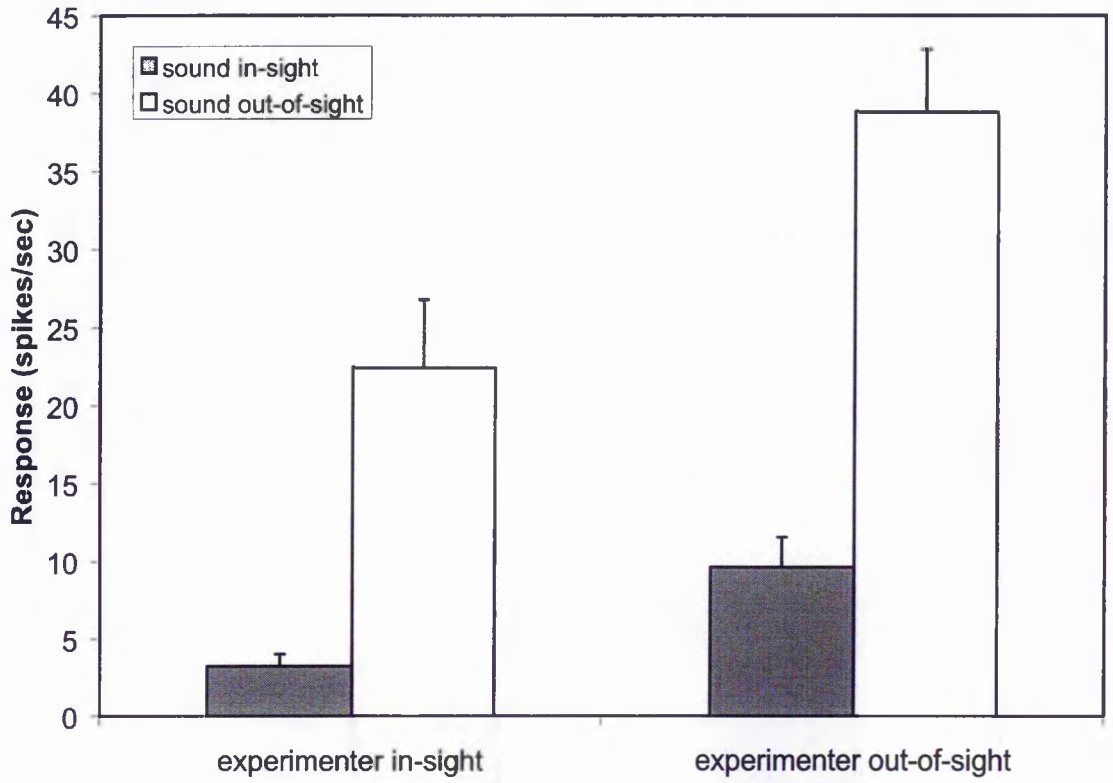


Figure 7.5 Responses of cell T28_3012 to different conditions of sound presentation. The sound was a mop striking a chair and responses are based on cell activity recorded for 0.5 seconds after production of the sound. The sound was produced either in- or out-of-sight, and the experimenter was either in- or out-of-sight. Two-way ANOVA with sound source visibility and experimenter visibility as factors shows a main effect of both sound source visibility ($F_{1, 16} = 59.16$, $p < 0.00001$) and experimenter visibility ($F_{1, 16} = 13.13$, $p < 0.0023$), but the sound source by experimenter interaction does not reach significance ($F_{1, 16} = 2.53$, $p > 0.13$). Post-hoc testing shows that the two conditions with the sound produced out-of-sight are significantly different from all other conditions and from each other. Each condition, n=5.

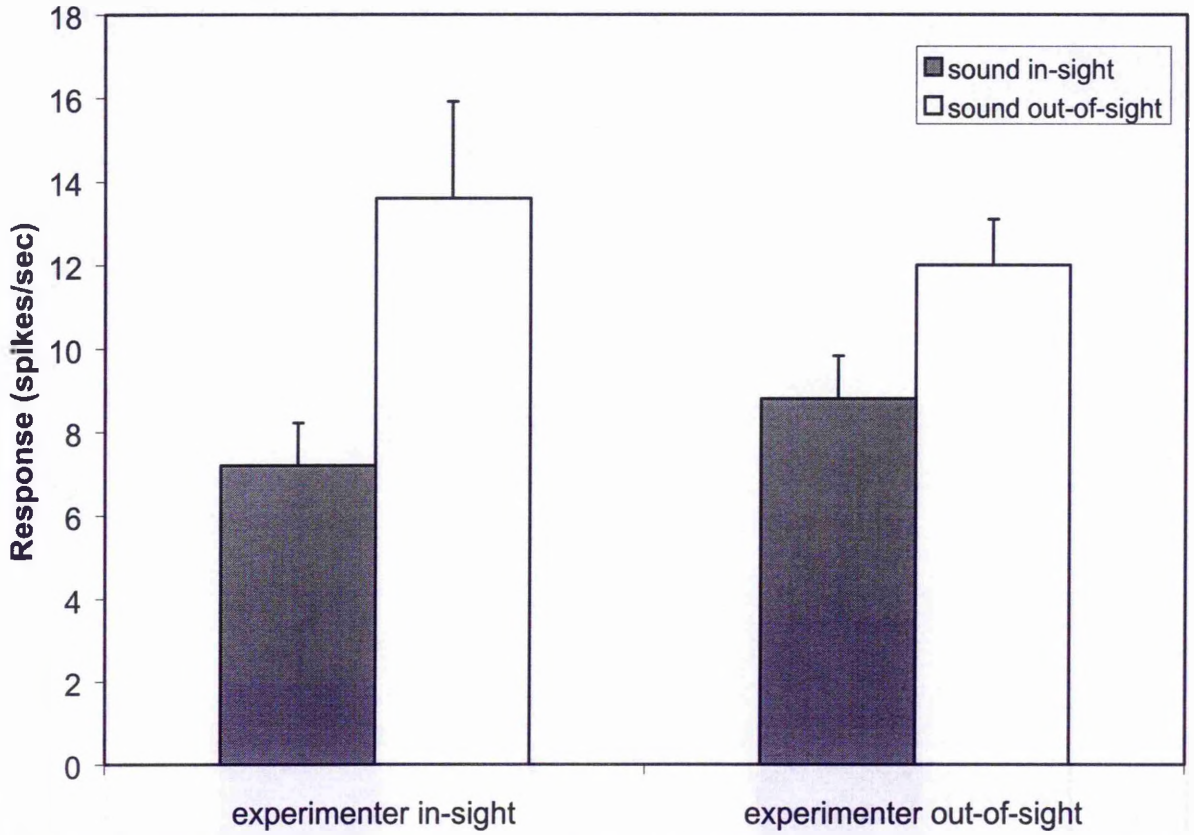


Figure 7.6 Responses of cell T25_2961 under different conditions of sound presentation. The sound (rustling of curtains) was produced either in- or out-of-sight and the experimenter was either in or out-of-sight. Responses are based on cell activity recorded for 0.5 seconds after production of the sound. Two way ANOVA with sound source visibility and experimenter visibility as factors shows a main effect of sound source visibility ($F_{1, 16} = 10.67$, $p < 0.005$), but no effect of experimenter visibility ($F_{1, 16} = 0.00$, $p>0.05$) and no interaction ($F_{1, 16} = 1.19$, $p>0.05$). Post-hoc testing shows that experimenter in sight, sound out-of-sight is significantly greater than experimenter in-sight, sound in-sight. There were no other significant comparisons. Each condition, n=5.

rustling) was out-of-sight than when the rustling was in-sight and the subject could see the curtains moving. The visibility of the experimenter (in- or out-of-sight) did not have a significant effect on the responses of the cell.

The data from these cells suggests that modulation of responses is greatest when the subject can see the movements producing the sound, although there may also be a general modulation when other objects, such as the experimenter, are in-sight. In both cell T28_3012 and cell T12_3068 there was a modulation of auditory responses with the experimenter in-sight compared with out-of-sight, even though the movements producing the sound were not visible.

7.3.3 Effect of position

The cells described in the previous chapter showed differential responses according to the position of the occlusion within the laboratory. Such positional selectivity was also observed in the cells described here. For example, the cell illustrated in figure 7.7 was tested with sounds produced in and out-of-sight at different locations around the laboratory. A two-way ANOVA with position (either on the left side of the room or in the centre) and visibility of sound source (either in- or out-of-sight) as factors shows a main effect of both position and visibility but no position by visibility interaction. Responses were greater when the sound was produced out-of-sight than in-sight and responses were greater for the left position than the central position. Responses were not recorded for sounds produced in-sight on the right, but there was no difference between central and right responses to sounds produced out-of-sight suggesting that there was not a gradual gradient of

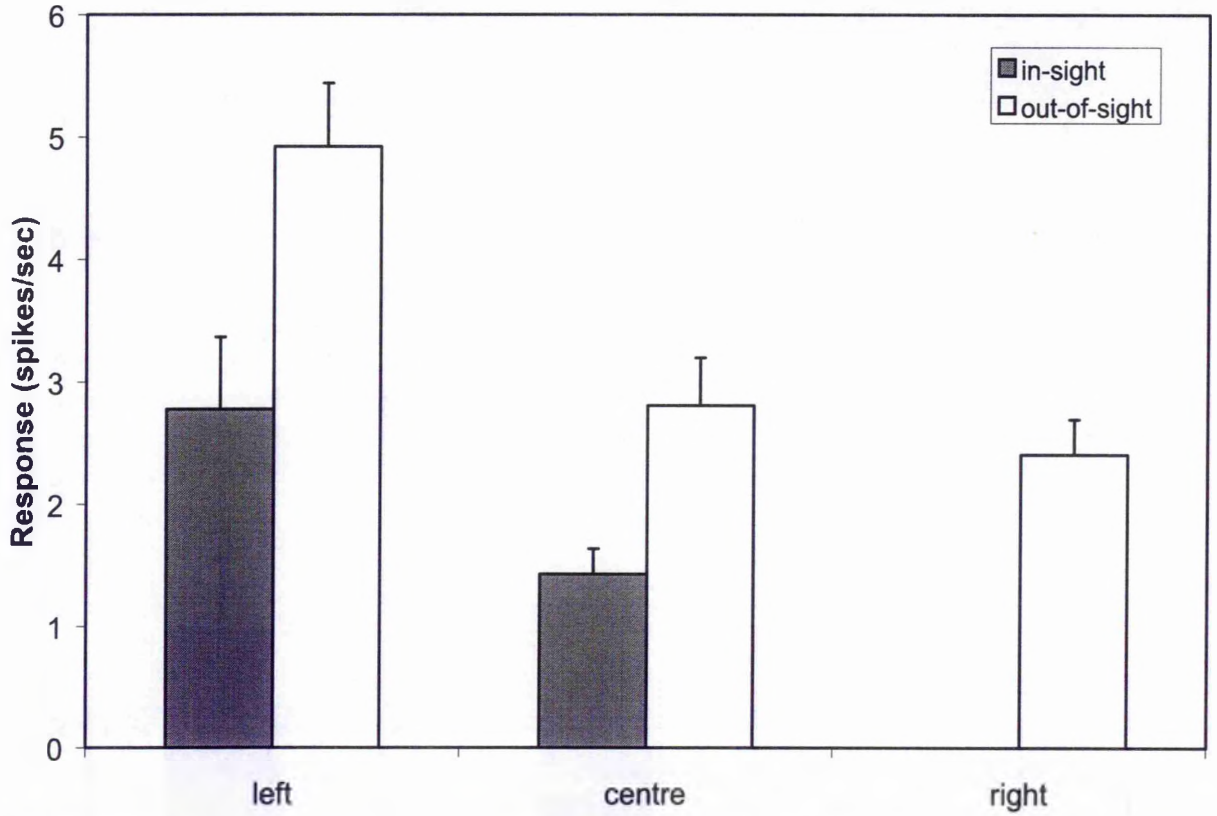


Figure 7.7 Responses of cell T32_2801a to sounds produced by the experimenter in and out-of-sight at different positions around the laboratory. The sound was tapping of the foot and responses are based on cell activity recorded for 2 seconds after the production of the sound. A two-way ANOVA on the responses for the left and centre conditions with position and experimenter visibility as factors shows a main effect of both position ($F_{1, 45} = 16.36$, $p < 0.00021$) and experimenter visibility ($F_{1, 45} = 16.93$, $p < 0.00017$) but no interaction between the two factors ($F_{1, 45} = 0.80$, $p > 0.37$). Post-hoc testing shows that out-of-sight left is greater than all other conditions. From left to right, n=9, 13, 14, 13, 11.

responsiveness across the laboratory from left to right, but rather a preferred location on the left.

Differential responses were also observed for sounds produced at different distances. The cell illustrated in figure 7.8 showed responses to sounds produced both near (1.5m) and far (4m) and gave greater responses to in-sight than out-of-sight sounds. The cell was tested at two different distances, both with and without sound. A two-way ANOVA with distance and sound production as factors shows a main effect of both distance and sound production, with a significant sound production by distance interaction. This shows that the cell responded to sounds produced both near and far, but that the response was much greater for near sounds than far sounds. This cell showed broad selectivity for the nature of sounds and differential responses were not observed for sounds differing in intensity. Not all cells, however, showed this distance effect. Figure 7.9 shows the responses of a cell to sounds produced both near (1.5m) and far (4m), in and out-of-sight. A two-way ANOVA on this cell shows a significant main effect of sound source visibility only. Sounds produced in-sight elicited greater responses than sounds produced out-of-sight, but the distance of the sound from the subject had no effect.

7.3.4 Eye movements

Eye movements were monitored during testing, and no simple relation was observed between eye movements or position and cell response. Responses were observed both when the monkey fixated the sound source and when the monkey was looking at other locations around the laboratory. Differential responses between

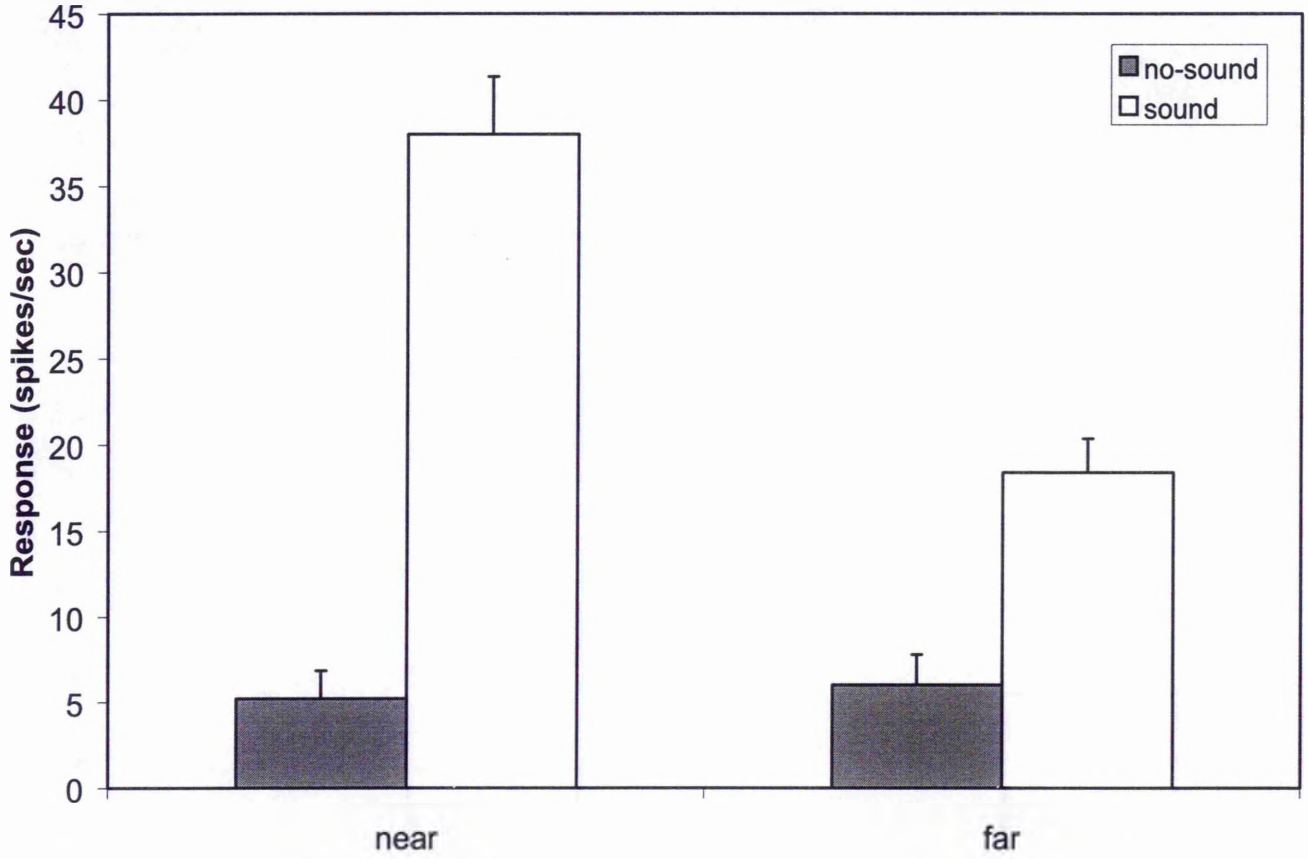


Figure 7.8 Responses of cell T32_2837 to sounds produced by the experimenter at different distances. Sound was tapping of the foot and responses are based on cell activity recorded for 500ms after the production of the sound. Near and far were 1.5m and 4m respectively. A two-way ANOVA with distance and sound as factors shows a main effect of both distance ($F_{1, 16} = 17.00$, $p < 0.0008$) and sound ($F_{1, 16} = 98.22$, $p < 0.00001$) with a significant distance by sound interaction ($F_{1, 16} = 20.01$, $p < 0.0004$). Post-hoc testing shows that near sound and far sound are significantly different from all other conditions and from each other. Each condition, n=5.

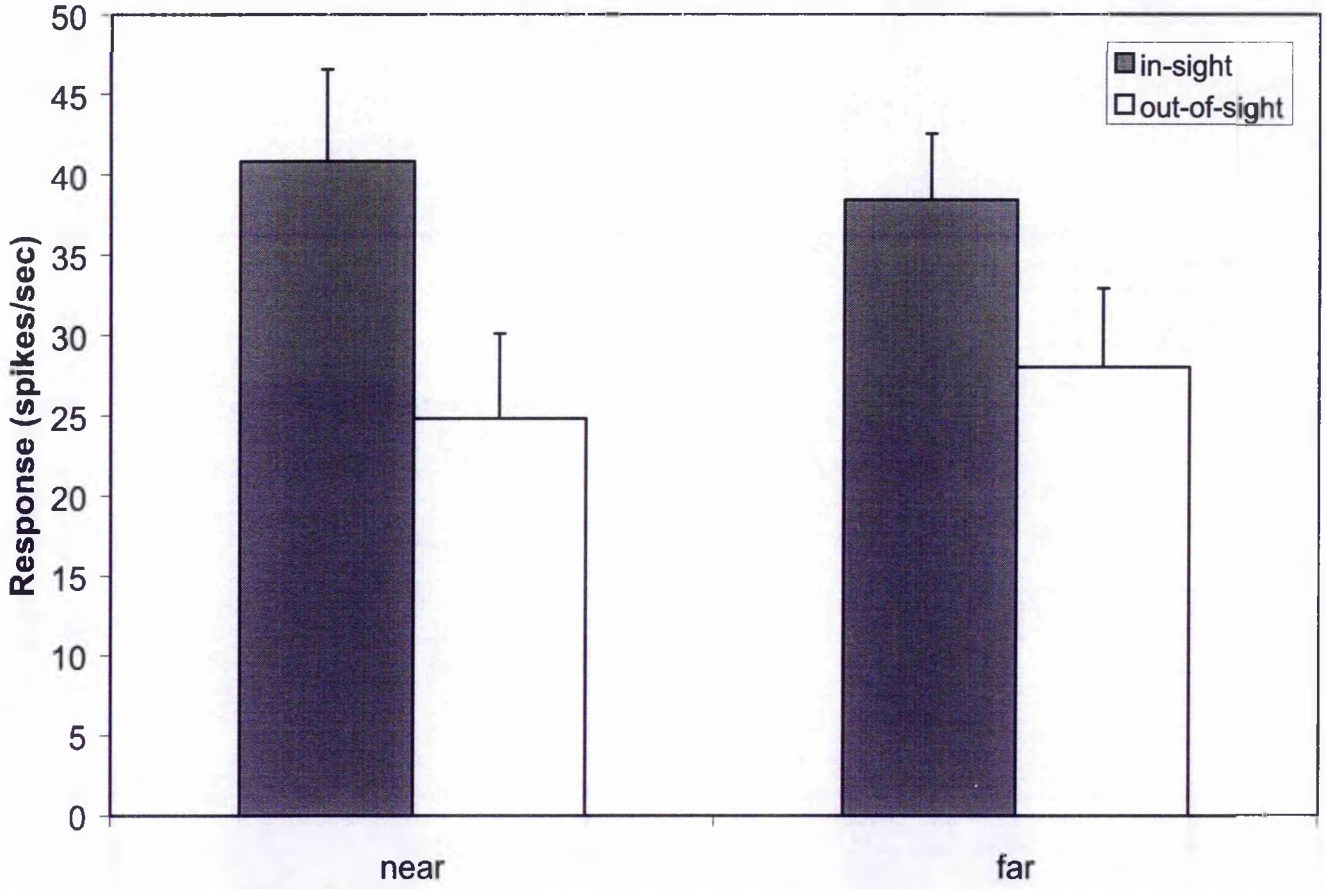


Figure 7.9 Responses of cell S101_2951 to sounds produced by the experimenter in- and out-of-sight at different distances from the subject. Sound was an imitation monkey call and responses are based on cell activity recorded for 250ms after production of the sound. A two-way ANOVA with distance and experimenter visibility as factors shows a main effect of visibility ($F_{1, 16} = 6.87$, $p < 0.019$), but no effect of distance ($F_{1, 16} = 0.006$, $p > 0.05$) and no distance by visibility interaction ($F_{1, 16} = 0.31$, $p > 0.05$). Each condition, n=5.

different testing conditions were observed despite similar patterns of fixations and eye movements.

7.3.5 Cell localisation

The x-rays taken at the end of each recording session (see appendix B) show that the cells described in the current chapter are co-extensive with those described in the previous chapter showing responses during the occlusion of visual stimuli. This confirms that the cells were located within the superior temporal sulcus. Moreover, the bimodal nature of responses suggests that the cells were located in the upper bank of the sulcus. The lower bank of the sulcus is generally regarded as a unimodal area (see chapter 2).

7.4 Discussion

The cells described in this chapter exhibited auditory-visual interactions. Differential responses were observed to sounds produced in- and out-of-sight. For 50% of the cells the response elicited by an auditory stimulus was greatest when produced out-of-sight and for the remaining 50% of cells the response was greatest for auditory stimuli produced in-sight. Interaction effects were observed to be maximal when the sound source and the movements producing the sound were visible. As with the cells reported in the previous chapter, there was some evidence for positional selectivity.

It could be argued that the responses observed might simply reflect the eye movements of the monkey. Responses were observed, however, both when the

monkey fixated the sound source and when the monkey was looking at other locations. Furthermore, differential responses were observed with similar patterns of fixations and eye movements. Such observations make it unlikely that eye movements alone could account for the responses (see also chapter 6).

The cells showing a greater response to sounds produced in-sight than out-of-sight are similar to the responses described by Bruce, Desimone and Gross (1981). They reported a small number of cells that fired only in response to both the sight and sound of an object hitting a surface and not to the sight or sound alone. Such cells did not respond to other non-related combinations of visual and auditory stimuli.

It could be argued that the differences in activity observed between the different conditions tested might reflect differences in the nature of the sound. Sound produced out-of-sight may be attenuated by the occluder, and sound intensity will vary with distance from the subject. These differences, however, are unlikely to explain the observed response differences. In cells T12_3068 (figure 7.1) and S101_2951 (figure 7.9), the shutter box was on the front of the chair in all conditions. All that varied between conditions was the transparency of the shutter, so there were no differences in the sound quality produced in the different conditions. Similarly, differences in sound quality cannot account for the differences between sounds produced out-of-sight at different positions (cell T32_2801a, figure 7.7) and with and without the experimenter in view (cell T28_3012, figure 7.5). In all cases any attenuation in the sound produced by the occluder is the same in all conditions. Furthermore, the cells tested showed very little selectivity for the nature of the sound, responding to a range of different sounds, and it is unlikely that the cells showed selectivity for intensity. Specifically, in the cell showing distance effects,

there was no clinically observed effect of varying the intensity of the sound at a fixed location.

The stimulus conditions used here are strikingly similar to those used by Mistlin and Perrett (1990) in presenting tactile stimuli. In that study, tactile stimuli were presented either in or out-of-sight and the cellular differentiation between these conditions was related to expectation. It was argued that seeing the approach of a visual stimulus leads to expected touch whereas touch out-of-sight is unexpected. Attenuated responses when the tactile stimulus was expected were reported. Such a distinction could also be made for the present stimuli. Sounds made in-sight could be regarded as expected because the movements that produce the sounds can be seen. On the other hand sounds made out-of-sight can be said to be unexpected because there is no prior indication that a sound is about to be made. Mistlin and Perrett (1990) found that responses to expected tactile stimuli were attenuated relative to responses to unexpected tactile stimuli. In terms of visual processing it makes sense to reduce the processing of expected stimulus events. For the present data such a distinction does not seem appropriate with some cells selective for "expected" and some for "unexpected" sound.

The selectivity for auditory-visual combinations shown by the cells reported here could enable differentiation of possible sound sources, for example, in the colony situation. Some cells would respond to sounds (e.g. threat) produced only by visible colony members while other cells would respond only to sounds produced out-of-sight. This may be particularly important in identifying the location of a predator or colony member hidden from view. The positional sensitivity observed in these cells may be important for eliciting appropriate behavioural responses (e.g. orienting or fleeing in the correct direction).

7.5 Summary

A small population of cells showing auditory-visual interactions was recorded in STSa. Such cells showed a modulation of responses to auditory stimuli depending on the concurrent visual stimulation. For some cells there was a greater response to auditory stimuli when the experimenter was out-of-sight and for other cells the converse was found to be the case. Modulation was greatest depending on the visibility of the sound source and the movements producing the sound. For two of the cells reported, the position of the auditory stimulus within the room was also found to be important in determining the cell response.

CHAPTER 8

POSITIONAL EFFECTS IN CELLS OF THE ANTERIOR SUPERIOR TEMPORAL SULCUS

8.1 SPACE AND THE VENTRAL BRAIN

8.1.1 Introduction

In the preceding two chapters, cell responses in the anterior superior temporal sulcus dependent on the position of the stimulus have been described. These effects are surprising given the predominant view (e.g. Ungerleider and Mishkin, 1982) that the ventral stream of cortical visual processing, of which the STSa is generally considered a part, is involved solely in the processing of object form. Analysis of object position/location is believed to be the domain of the dorsal proccessing stream that includes areas of the parietal cortex. Milner and Goodale (Milner and Goodale, 1993, 1995; Goodale and Milner, 1992), however, have suggested an alternative distinction that predicts that spatial information is contained within the ventral stream (see chapter 2). Emphasising the outputs of the visual system, they have proposed a division between visuomotor function (visual analysis for action) and object identification (visual analysis for recognition). Thus, both streams are concerned with object identity and location, but for different purposes. Action requires an egocentric reference frame whereas aspects of recognition may depend on an allocentric reference frame.

Functional imaging studies (e.g. Owen *et al.*, 1996; Maguire *et al.*, 1996b, 1997,1998a, b), neurophysiological studies (e.g. O'Keefe, 1979; Tamura *et al.*, 1992; Rolls *et al.*, 1997; Suzuki *et al.*, 1997) and lesion studies in both humans (e.g. Maguire *et al.*, 1996a; Smith and Milner, 1981) and non-human primates (e.g. Parkinson *et al.*, 1988; Angeli *et al.*, 1993) have all implicated areas of the ventral brain in the processing of spatial information. The hippocampus has been the focus of much work on spatial function, but it is now clear that regions outside the hippocampus in ventral areas of the brain are also involved in spatial representation.

In this chapter I will briefly discuss some of the evidence for spatial function in ventral brain areas before presenting further neurophysiological evidence for analysis of spatial position in STSa. By ventral brain, I mean brain areas within the temporal lobe, including temporal cortex and medial brain structures such as the hippocampus and amygdala.

Evidence for ventral brain involvement in spatial functioning falls largely into two broad areas:

(1) Simple spatial function involving basic analysis of the spatial position of objects

(2) Navigation/topographical orientation, the use of spatial information to guide movement around the environment

These two areas reflect the types of task that have been used in investigating spatial function and do not necessarily imply different neuronal mechanisms or involvement of different brain areas.

8.1.2 Neurophysiological studies

In the hippocampus and parahippocampal gyrus of both rats (O'Keefe and Dostrovsky, 1971; O'Keefe, 1976; O'Keefe, 1979) and non-human primates (Rolls *et al.*, 1989, 1997, 1998; Rolls and O'Mara, 1995; Ono *et al.*, 1991, 1993; Tamura *et al.*, 1990, 1992; Feigenbaum and Rolls, 1991), neurones have been found with responses related to many different aspects of the spatial environment (see O'Mara, 1995 for a comparative review). Place cells in rats (O'Keefe and Dostrovsky, 1971; O'Keefe, 1976; O'Keefe, 1979) fire when the animal is in a particular location in the environment. The activity of these neurones is not related to motor behaviour, but to distal sensory cues available in the environment (e.g. O'Keefe and Conway, 1978; Olton *et al.*, 1978). Such place cells have also been identified in non-human primates (Ono *et al.*, 1991, 1993; Nishijo *et al.*, 1997), although in studies by Rolls and colleagues, no such cells have been observed (Rolls *et al.*, 1998) and the status of the reported place cells as analogues of those in the rat has been questioned (O'Mara, 1995).

Many primate hippocampal neurones respond to the presentation of visual and auditory stimuli (e.g. Tamura *et al.*, 1990; Vidyasagar *et al.*, 1991) and may be directionally selective, responding only to stimuli moving in a particular direction (Tamura *et al.*, 1990, 1992), or positionally selective, responding only to stimuli presented at a particular position in space (Feigenbaum and Rolls, 1991). Analysis of the spatial reference frame of these cells (by moving/rotating the monkey and/or the position of the stimulus) has shown both egocentric and allocentric coding of space (Tamura *et al.*, 1990, 1992; Feigenbaum and Rolls, 1991), although allocentric coding may be more common (Feigenbaum and Rolls, 1991). Primate hippocampal

neurones have also been found to be responsive to where the monkey is looking in the environment regardless of the head direction or the position in space of the monkey (Rolls and O'Mara, 1995, Rolls *et al.*, 1997). Such neurones often continue to respond when the spatial view is obscured (Robertson *et al.*, 1998) suggesting that proprioceptive and vestibular cues are important.

The hippocampus has been proposed as a site for the storage of allocentric spatial representations (O'Keefe and Nadel, 1978) and may play a crucial role in navigation. Head direction cells in the rat and primate fire when the head is orientated in a particular direction (rat: e.g. Taube, 1998; primate: Rolls *et al.*, 1998) and some cells in the primate have been found to respond during whole-body motion (O'Mara *et al.*, 1994). Such properties would be useful in navigating a spatial environment.

The activity of hippocampal and parahippocampal units in primates has also been recorded during the performance of spatial delayed response and object-place memory tasks (Watanabe and Niki, 1985; Cahusac *et al.*, 1989), tasks that have commonly been used in lesion studies (see section 8.1.3a). In the spatial delayed response task, the monkey is presented with a cue stimulus and then after a delay with two choice stimuli, one of which is in the same location as the cue. The monkey's task is to respond to the choice stimulus that is in the same location. In the object-place memory task the monkey is shown a sample stimulus in one location of a computer screen. After a delay, the monkey is presented with a same or different stimulus in the same or different position and has to respond only when the object and place are the same as during the cue period. Hippocampal and parahippocampal units were found to be active during all stages of both types of task, and many units had differential activity depending on the location of the cue stimulus. In the object-

place task, a small number of neurones were found to respond to a combination of object and place.

Recently, Suzuki *et al.* (1997) recorded from neurones in the entorhinal cortex of macaques during the performance of delayed matching to sample and delayed matching to place tasks with intervening stimuli. In these tasks the monkey has to remember an object or a spatial location across delays and intervening stimuli. The results were similar to those obtained in previous studies in prefrontal and inferotemporal cortex (for review, see Desimone *et al.*, 1995; Desimone, 1996). In both tasks, neurones were found with activity selective for the objects or places presented, and selective activity was also observed during the delay periods. Differential responses were also observed in some neurones to the test stimuli depending on whether or not they matched the stimuli held in memory in terms of form or position. These results suggest an involvement of entorhinal cortex in both spatial and object-related functions related to short-term memory. The monkeys performed either an object or a place memory task and therefore it was not possible to determine if the neurones would show selectivity for a combination of both object and place.

8.1.3 Lesion studies

(a) Non-humans

Rats with hippocampal lesions are impaired on spatial tasks such as the water maze (e.g. Morris *et al.*, 1982) which requires the use of distal cues to navigate a spatial environment. Similar deficits may also be observed in rats after perirhinal

and/or entorhinal cortex lesions (e.g. Schenk and Morris, 1985; Wiig and Bilkey, 1994; Nagahara *et al.*, 1995).

In monkeys, a consistent finding has been the lack of impairment on the spatial delayed response task following hippocampal lesions (e.g. Mishkin, 1954; Orbach *et al.*, 1960; Mahut, 1971) with delays of up to 10 seconds. In the version of the delayed response task commonly used, one of two (or more) food wells is baited and the wells covered with identical objects. After a delay period during which time the wells are occluded from the subject's view, the subject is allowed to reach out and retrieve the object. The task requires memory for a location. The length of the delay, however, may be critical. Zola-Morgan and Squire (1985) found that amygdalo-hippocampectomized monkeys were unimpaired at delays of 8s, but showed increasing impairment with delays of 15 and 30s. In contrast, Correll and Scoville (1967) found no evidence for a significant impairment with delay intervals of up to 60s and concluded that the length of delay was unimportant.

Impairment following hippocampal lesions is seen, however, in variants of the standard delayed response task (Parkinson *et al.*, 1988; Angeli *et al.*, 1993). For example, Parkinson *et al.* (1988) trained monkeys preoperatively on a modified version of the delayed response task (see figure 8.1) in which, during sample presentation, two out of three wells were covered with two different objects. After a six second delay the monkey was presented with one of the sample objects and a duplicate presented over either:

(a) the same two wells as during sample presentation

(b) one of the two wells used during sample presentation and over the third well

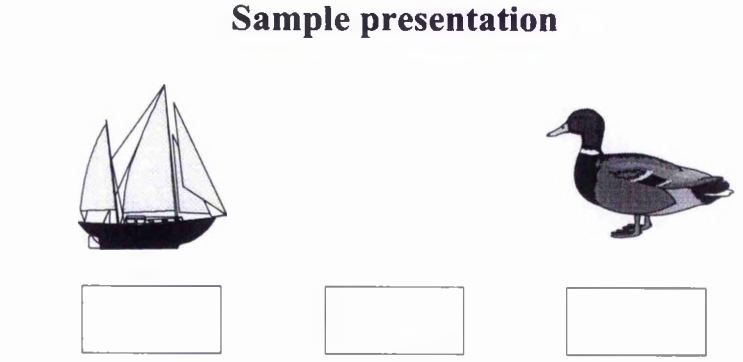


Figure 8.1 Summary of the task conditions used by Parkinson *et al.* (1988). For correct performance of the object-place trials the monkey must remember the conjunction of object and place presented in the sample presentation period. By contrast, in the place only trials, all that is required for correct performance is a memory of the locations used during sample presentation.

To solve version (a) of the task and receive a reward, the monkey must remember the conjunction of object and place and respond to the object in the position used during sample presentation. In contrast, to solve version (b) of the task, the monkey need only remember the two locations of the objects and respond to the same location as used during sample presentation.

Postoperatively, monkeys with hippocampal lesions were impaired on both versions of the task. The deficit was interpreted as impairment in object-place memory, the association of an object and a place. The monkeys may have failed on version (b) of the task because during sample presentation there was no distinction between the trial types and they may have used the same strategy. Gaffan and Saunders (1985) reported similar deficits for object-place memory following transection of the fornix in a running recognition task.

The deficit, however, may be a more fundamental deficit in place memory and not specifically in object-place memory. Angeli *et al.* (1993) trained monkeys preoperatively on a similar task to Parkinson *et al.* (1988) but object-place memory was never required (figure 8.2). During sample presentation, 2 out of three wells were covered with objects (either identical or different). After a delay, the monkeys were allowed to choose between two wells (one of which was the same as during sample presentation) covered with identical objects (one of the objects used during sample presentation). To receive the reward the monkey had to look under the object that was in the same location as during sample presentation. Performance requires memory for the two locations used during sample presentation only. The nature of the objects is irrelevant for successful performance. Postoperatively, monkeys with hippocampal lesions showed impaired performance equivalent to that reported by Parkinson *et al.* (1988). Given the lack of impairment on the standard delayed

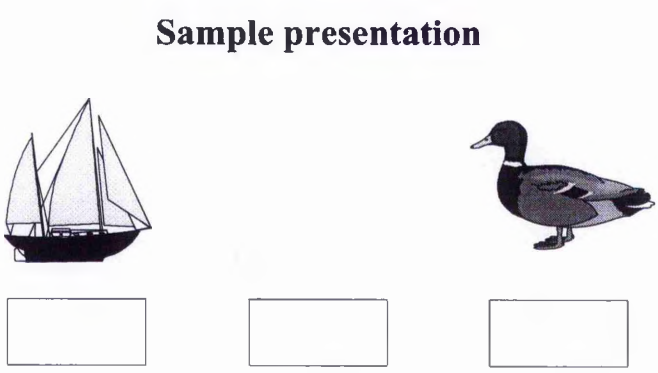


Figure 8.2 Summary of the task used by Angeli *et al.* (1993). For correct performance of the task all the monkey has to remember is the locations of the objects in the sample presentation period. The nature of the objects is irrelevant for task performance.

response task, this study suggests that hippocampectomized monkeys can remember one but not two places and that hippocampectomy does not specifically impair object-place memory.

Impairments after hippocampectomy have also been reported in spatial delayed alternation (Orbach *et al.*, 1960; Pribram *et al.*, 1962; Waxler and Rosvold, 1970; Mahut, 1971) and spatial reversal tasks (Mahut, 1971), but not object reversal or non-spatial delayed alternation (Mahut, 1971).

Although the lesions in all the studies described above involve the hippocampus there is much variation in the extent of the lesions. Some studies selectively removed the hippocampus (e.g. Angeli *et al.*, 1993), while others lesioned both hippocampus and amygdala (e.g. Zola-Morgan and Squire, 1985). Typically, there is also damage to many other structures. For example, the lesions reported in Parkinson *et al.* (1988) also included the parahippocampal gyrus and parts of the entorhinal cortex. In some subjects there was also damage to parts of the inferior temporal cortex. All lesions for the monkeys reported in the study of Zola-Morgan and Squire (1985) included the hippocampus and amygdala, the parahippocampal gyrus and entorhinal cortex. It is possible that areas outside the hippocampus in the ventral part of the brain also contribute to performance in spatial tasks. Waxler and Rosvold (1970) reported variable effects of hippocampal lesions on delayed alternation learning and retention with some monkeys showing impairment and others not. They interpreted the results in terms of different strategies used by different monkeys. Although there was quite a lot of variation in the extent of the lesions, they reported no relation between the extent of the lesions and performance. They found no group effects comparing pre- and post-operative performance on learning and retention except in a group of subjects with lesions of the entire

temporal lobe. The majority of these subjects required more trials to learn the task postoperatively than preoperatively and half the subjects failed to relearn the task at all. By comparison all subjects with selective hippocampal lesions relearned the task postoperatively with 2 out of 3 subjects requiring less trials than preoperatively. Thus areas outside the hippocampus and possibly in the temporal neocortex may be involved in spatial delayed alternation performance.

Recently, Thornton *et al.* (1998), found that monkeys with aspirate lesions of the hippocampus (including parahippocampal cortex) were more impaired on a spatial memory task than monkeys with ibotenic acid lesions of the hippocampus in which there was little extrahippocampal damage. This suggests that brain regions outside the hippocampus (e.g. adjacent parahippocampal and entorhinal cortex) are critically important in location memory.

(b) Humans

Patients who have undergone temporal lobectomies are often found to suffer from impairments in spatial memory tasks (e.g. Smith and Milner, 1981, 1984, 1989; Pigott and Milner, 1993; Feigenbaum *et al.*, 1996; Owen *et al.*, 1995; Abrahams *et al.*, 1997). The deficit is specific to the right temporal lobe (e.g. Smith and Milner, 1981), and is not found in subjects with left temporal lobectomies. The lesions typically involve the hippocampus and some areas of the overlying temporal neocortex. The extent of deficit is found to correlate with the extent of hippocampal removal (Milner, 1980) and, thus, the impaired abilities have been related to hippocampal function. Subjects with right anterior temporal lobectomies are also often impaired on the recognition and recall of visual patterns and objects (e.g.

Kimura, 1963; Milner, 1968; Pigott and Milner, 1993), but in most cases the extent of the deficit and the extent of the lesion are unrelated, suggesting that the critical area of damage may be neocortical and not hippocampal (Milner, 1980). There is in some studies, however, evidence for spatial deficits that do not correlate with the extent of hippocampal removal. For example, Smith *et al.* (1995) tested temporal and frontal lobectomy patients on a spatial memory task involving recall of the location of pictures presented on a computer screen. Both patient groups performed less accurately than controls, and for the temporal lobe group performance was not related to the extent of hippocampal damage. Those subjects with large lesions of the hippocampus performed at the same level as those with small lesions. In the same way that the visual pattern/object deficits have been localised to the temporal neocortex on the basis of the lack of correlation between extent of hippocampal damage and extent of deficit, so these results suggest that there may also be spatial functions dependent on temporal neocortex. An alternative interpretation, however, is that only a small amount of hippocampal damage is needed to produce such deficits (e.g. see Owen *et al.*, 1996). Such an interpretation, however, conflicts with the interpretation of visual pattern/object deficits also seen in patients with temporal lobectomies.

Pigott and Milner (1993) tested subjects with unilateral temporal or frontal lobe excisions on tasks involving delayed recognition memory for aspects of complex visual scenes. Subjects were required to state whether there were any changes in a visual scene compared with an earlier presentation of the same scene. There were five possible transformations of the visual scene: (a) inventory - one object in the visual scene was replaced by another object; (b) figurative detail - as inventory but replacing object differed form the original object only in figurative

detail e.g. pattern on object changed; (c) displacement - one object moved in the horizontal plane; (d) deletion - one object removed from the picture; and (e) object location - two objects within the scene interchanged. Only subjects with lesions of the right temporal lobe including large hippocampal damage were impaired on the object location condition (e) relative to controls. Subjects with right temporal-lobe lesions were impaired on the figurative detail and inventory conditions and there was no relation with the extent of hippocampal damage. Subjects with right temporal lesions, however, were also impaired on the displacement and deletion conditions. In these cases there was also no relation between the deficit observed and the extent of hippocampal damage implicating the right temporal neocortex in recognition memory for spatial composition. Subjects with left temporal lobe lesions (including either small or large hippocampal damage) were also impaired on the deletion condition. Pigott and Milner (1993), however, accounted for this deficit by suggesting that "spatial composition is encoded in terms of the pattern of empty and filled space in the scene, rather than in terms of the relative location of the objects". This interpretation relates the deficit to the visual pattern deficit that has been attributed to damage to the anterior temporal neocortex (e.g. Milner, 1980).

Ploner *et al.* (1998) found that subjects with hippocampal lesions that included the overlying neocortex were impaired on a task involving saccadic eye movements to remembered target positions whereas those with lesions restricted to the hippocampal formation were unimpaired relative to controls. This again implicates areas outside the hippocampus in the ventral part of the brain in spatial memory processing.

Topographical disorientation or impaired ability to navigate in a spatial environment has been reported in a number of brain-lesioned patients (e.g. see De

Renzi, 1982; Landis *et al.*, 1986; Habib and Sirigu, 1987). The nature of deficit across different patients is heterogeneous and the deficit has often been broken down into impairment of different functions. One such distinction (Farrell, 1996; Maguire 1997) has been between topographical amnesia (or inability to form topographical maps e.g. Bottini *et al.*, 1990) and topographical agnosia (or inability to recognise landmarks for navigation e.g. Landis *et al.*, 1986). Such a distinction, however, is not clear (Farrell, 1996; Suzuki *et al.*, 1998). An alternative distinction which parallels Ungerleider and Mishkin's (1982) division of the cortical visual system (see chapter 2) has been proposed by Levine *et al.* (1985 - see also Farrell, 1996) who distinguished between impaired object representations and impaired spatial representations. For example, patients may exhibit topographical disorientation because they are unable to recognize landmarks or because they are unable to orientate themselves with respect to such landmarks.

The ventral brain appears to play a critical role in topographical orientation. In the 16 cases reported by Landis *et al.* (1986), all patients had a posteromedial right hemispheric lesion (with at least 3 including an additional left-sided lesion). The critical lesion overlap in the four cases reported by Habib and Sirigu (1987) is the area of the parahippocampal gyrus (see also Milner and Goodale, 1995; Aguirre *et al.*, 1998). Additionally, topographical disorientation is often seen in association with prosopagnosia (e.g. Landis *et al.*, 1986) a deficit believed to arise through damage to temporal neocortical areas (e.g. Milders and Perrett, 1993).

Maguire *et al.* (1996) tested subjects who had undergone unilateral temporal lobectomies on tasks requiring topographical orientation. Subjects watched a video showing two overlapping routes through a novel urban environment and, after reaching criterion on a test of scene recognition for locations in the videos, were

required to perform tasks in which their memory for the environment and the spatial relations were taxed. Such tasks involved, for example, estimating the distance between landmarks, describing a route between landmarks, or sketching the urban environment. On all tasks, except one, left and right temporal lobectomy subjects were impaired relative to controls but there was no difference between the left and right groups. In the remaining task, the right temporal lobe group was impaired relative to controls.

Topographic disorientation can arise, however, from lesions in other brain areas including parietal cortex (e.g. Suzuki *et al.*, 1998), supporting the notion (based on the Ungerleider and Mishkin model of cortical visual processing) that impairment of either object processing or spatial processing underlies the disorientation (Levine *et al.*, 1985).

In reviewing the literature on topographical disorientation, Farrell (1996), argued that the available evidence does not support a dichotomy between spatial and object processing. Instead he proposed that the deficits arise from damage to an allocentric coding system located in the ventral stream. The dorsal stream may operate by continually updating the egocentric reference in relation to the allocentric reference frame, thus accounting for the deficits observed following parietal lesions.

8.1.4 Functional imaging

A number of functional imaging studies (see Milner *et al.*, 1997; Maguire, 1997; and Aguirre *et al.*, 1998 for recent reviews) have tried to establish the different areas of the brain involved in spatial processing. Many of these studies have implicated structures of the temporal lobe.

In a comparison of object and spatial encoding and retrieval, Owen *et al.* (1996) found an increase in rCBF in a region of the right parahippocanpal gyrus (corresponding to the entorhinal cortex) relating to the retrieval of object-location, but not location alone. In two separate "encoding" conditions, subjects saw pairs of white squares, either both unfilled or both containing an object. In the corresponding "retrieval" conditions the subjects again saw pairs of white squares, but for one square there was either an incorrect combination of object and position (object filled squares), or an incorrect location (unfilled squares) compared with the stimuli presented during encoding. Subjects had to respond to the correct location. Activation of the right parahippocampal gyrus was observed when the retrieving location condition was subtracted from the retrieving object-location condition. Although not commented on by the authors, subtraction of the retrieving location condition from the encoding location condition revealed activation in the inferior temporal gyrus, implicating this ventral brain area in the encoding of location.

The region of the parahippocampal gyrus has also been implicated in functional imaging studies of topographical learning (Aguirre *et al.*, 1996; Maguire *et al.*, 1996; Maguire *et al.*, 1998) and topographical memory (Aguirre *et al.*, 1996, Maguire *et al.*, 1997). For example, Aguirre *et al.* (1996), using fMRI, scanned subjects while they learned about a virtual 3D environment adapted from a computer game, and subsequently while the subjects had to retrieve information about that environment to navigate between two locations. In a control condition subjects moved through a single looping corridor with little topographic detail. That representations of the environment had been formed was tested by asking the subjects to sketch a map before the retrieval tasks were given. For both learning and retrieval, comparison of the test conditions with the control condition yielded activity

in the parahippocampal gyrus (including entorhinal cortex, parahippocampal cortex and perirhinal cortex). Three subjects showed bilateral activity, and 6 unilateral activity (3 left hemisphere, 3 right hemisphere).

Navigation in recently learned virtual environments, however, may not engage the same processes as those used in real-world situations. To examine topographical memory for real-world environments, Maguire *et al.* (1997) performed PET studies in which London taxi drivers had to recall either particular routes or particular landmarks in London. Comparison of the activity in these two conditions revealed significant activation of the right hippocampus. The right hippocampus was also implicated in a study in which subjects performed spatial retrieval tasks in a complex virtual computer-simulated town (Maguire *et al.*, 1998).

Interestingly, a number of functional imaging studies have failed to show any activation of the hippocampus in spatial tasks (e.g. Aguirre *et al.*, 1996; see also Milner *et al.*, 1997; Maguire, 1997). It has been suggested that such an absence results from equal activation of the hippopcampus in the test and control tasks, so that the activity is effectively subtracted out (Maguire, 1997).

8.1.5 Summary

Converging evidence from neurophysiology, functional imaging and lesion studies suggest that extrahippocampal sites, and in particular the parahippocampal cortex and entorhinal cortex, are critical sites for spatial analysis. The available evidence, however, does not preclude a role for temporal neocortical areas and many studies suggest their involvement. In particular, the evidence from the study of

topographical disorientation suggests an involvement of areas of temporal neocortex and the ventral stream in complex spatial behaviour.

8.2 Further neurophysiological evidence

There have been a few previous reports of cells in STSa with responses that could be interpreted in terms of spatial sensitivity (see chapter 2). For example, cells responsive to reaching movements (e.g. Perrett *et al.*, 1989) have been found to respond in a goal-directed manner (see chapter 2) where the goal might be an object or a spatial position. Such cells responded to arm movements that brought the experimenter's arm to a particular location in which a target object was positioned, but not to equivalent arm movements to different positions. The observed responses were independent of the spatial position of the experimenter, and the direction of the arm movement.

Similarly, cells have been reported that responded to movement of the experimenter but only when that movement was directed towards one of two doors of the testing room (Perrett *et al.*, 1990; see chapter 2). The responses were the same even with the primate chair rotated so that the monkey was now facing in a different direction.

Such responses require coding of the spatial relationship between the experimenter and the object or position and are much more likely to be achieved in an allocentric spatial framework. Although the same computation could be performed in an egocentric framework, the analysis is much more complicated (see chapter 2).

In a study of visual and somatosensory properties of neurones (Mistlin and Perrett, 1990), cells with qualitative changes in response as the distance of the visual stimulus from the subject was increased were reported. These distance effects, however, were not extensively studied (Perrett, personal communication).

Given the position sensitivity observed in the cells described in chapters 6 and 7, other cells recorded in the same recording sessions were re-examined for evidence of spatial coding. The aim was to determine if spatial sensitivity is more extensive in STS, or restricted to a subset of cells.

8.3 Methods

Cells were tested clinically as described in the general experimental methods (see chapter 5). All cells were tested using the shutter box for controlled presentation with a minimum of 5 trials per condition. Stimuli (live, slide or laserdisc images) were presented in a pseudorandom order with each presentation lasting 1 second. Firing rates are based on a 500ms period beginning 100ms after the onset of the stimulus (corresponding to the average latency observed for cells in anterior STS - Oram and Perrett, 1992). Positional effects were not systematically tested for, and protocols had to be adapted to suit the selectivities of individual cells. Thus there is substantial variation in the testing of the cells and further relevant methods will be discussed as appropriate in the context of individual cells. Responses were analysed using one and two-way ANOVAs (as appropriate) and Tukey post-hoc tests with level of significance $p < 0.05$ throughout.

8.4 Results

8.4.1 General results

Out of 463 cells recorded in the anterior superior temporal sulcus, 71 (15%) were observed to be sensitive to the position of stimulus presentation within the laboratory. This figure is likely to be an underestimate since the effect of position was not tested for all cells. The figure includes the thirty cells showing increasing levels of activity as an object moves out of sight that were described in chapter 4 and the two auditory-visual cells with positional sensitivity described in chapter 5.

Here, I will concentrate on the remaining 39 cells. These 39 cells showed a variety of response properties, responding to many different categories of stimuli (e.g. static, moving, arm movements).

8.4.2 Distance effects

The most prominent observation of positional sensitivity was that relating to distance of the stimulus from the subject. The responses of 35 cells were found to vary according to the distance of the visual stimulus from the subject. For 25 cells, responses were greater when the stimulus was close to the subject (<2m) than when the stimulus was further away (2-4m). The two cells illustrated in figures 8.3 and 8.4 were tested with live static human figures at three distances (1m, 2.5m and 4m). Both cells showed a differential response with distance, with greater responses when the stimulus was at 1m than at 2.5m and 4m. For the cell in figure 8.3, there is still a

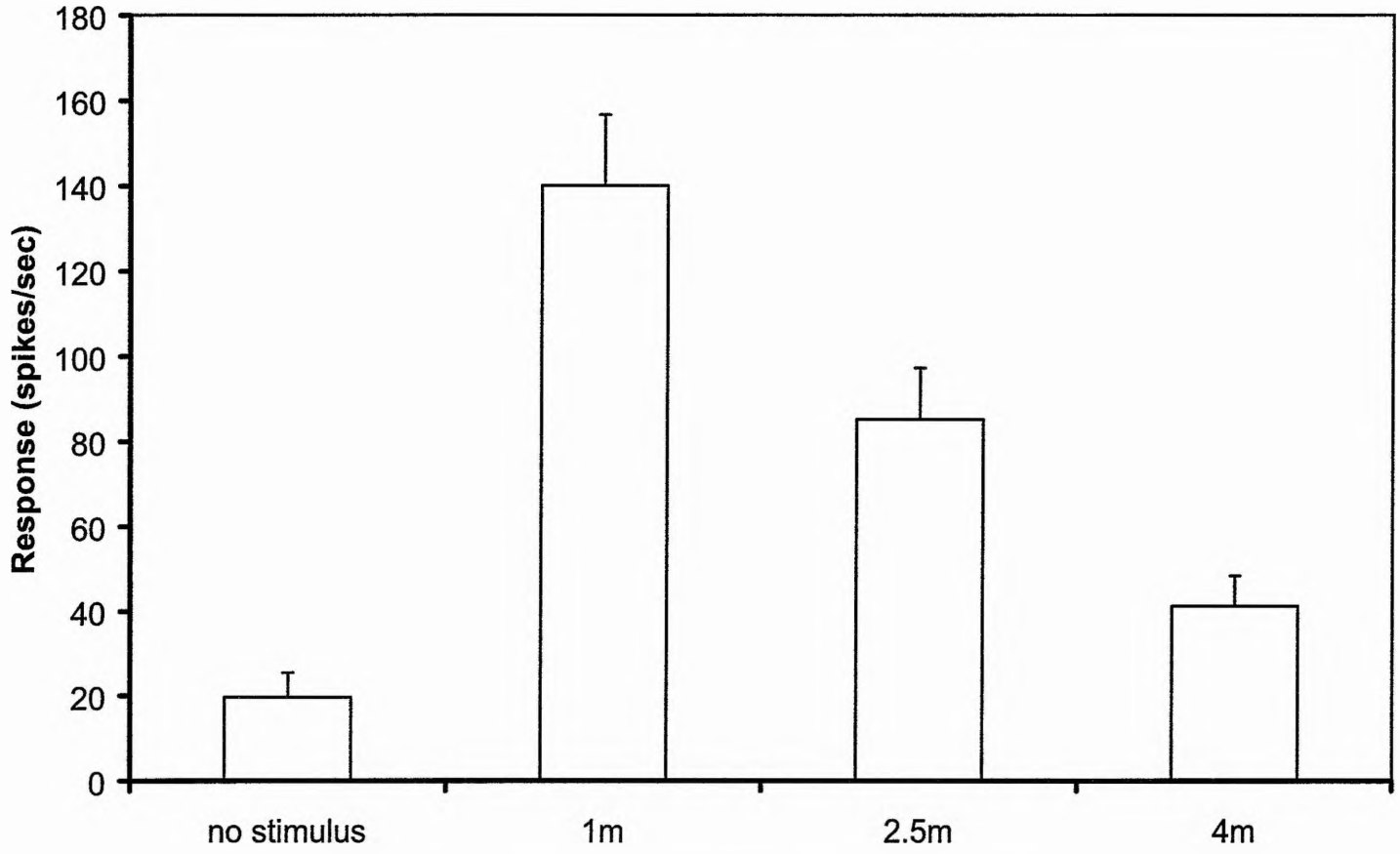


Figure 8.3 Responses of cell T18_3235 to a static human at different distances (One-way ANOVA: $F_{3, 16} = 22.4$, $p < 0.00001$). Post-hoc testing shows that the responses at 1m and 2.5m are significantly greater than spontaneous firing (no stimulus) and that the response at 1m is significantly greater than the response at 4m. Each condition, n=5.

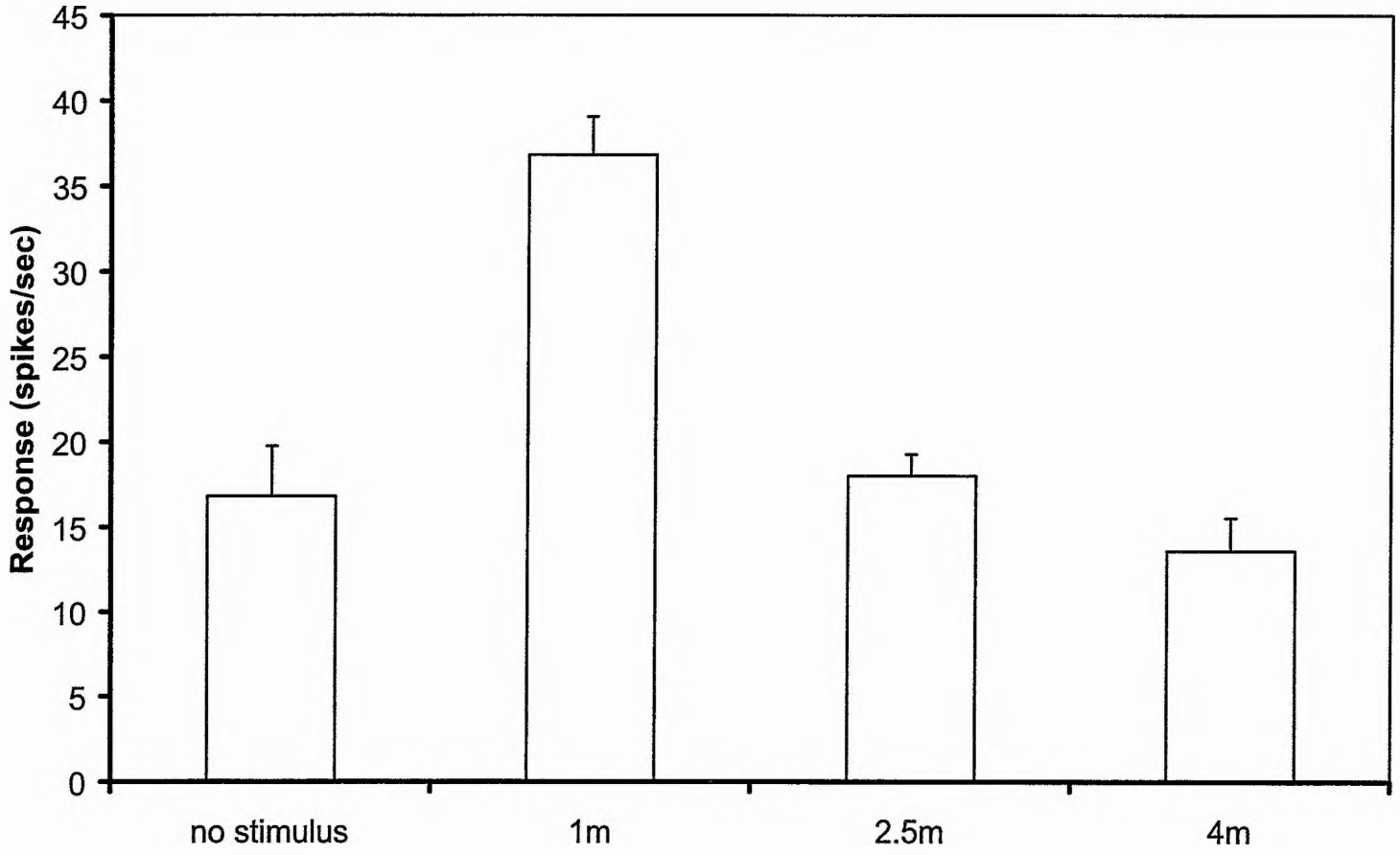


Figure 8.4 Responses of cell T10_3092 to a static human at different distances (One-way ANOVA: $F_{3, 16} = 23.2$, $p < 0.00001$). Post-hoc testing shows that the response at 1m is significantly greater than all other conditions. Each condition, n=5.

response to the stimulus at 2.5m (relative to the spontaneous firing rate), but the response is reduced relative to that with the stimulus at 1m.

For 9 cells the opposite effect was observed with a preference for stimuli presented further away (> 2m) than close (< 2m) to the subject. For example, the cell illustrated in figure 8.5 was tested with a live static human figure presented at the same three distances as the cells in figures 8.3 and 8.4. For this cell, however, there is no response to the static human (relative to the spontaneous firing rate) at 1m or 2.5m, but there is a strong response to the static human when presented at the far end of the laboratory (4m).

The majority of cells showed either an increase or a decrease in responsiveness with increasing distance of the stimulus from the subject. One cell, however, presented with a live static human at 0.5m, 1m, and 3m from the subject gave the greatest responses with the stimulus presented at 1m (figure 8.6). The cell was tested with both front and back views of the head, but there was no difference in responses between these two views.

Distance effects, such as these, were observed both for cells responding to static stimuli and for cells selectively responsive to movement. All the cells described so far were responsive to static stimuli. The cell illustrated in figure 8.7, however, was responsive to arm movements/reaching movements made in the direction of the subject. The arm movements were made in isolation without any target object for the action. The distances in this case refer to the position of the body of the experimenter when the reaching movement was made. At all three distances there was a significant effect of the reaching movement (relative to the spontaneous firing rate), but the response was greater with the experimenter at 1.5m than at 2.5m from the subject. The comparison between 1.5m and 4m just fails to reach

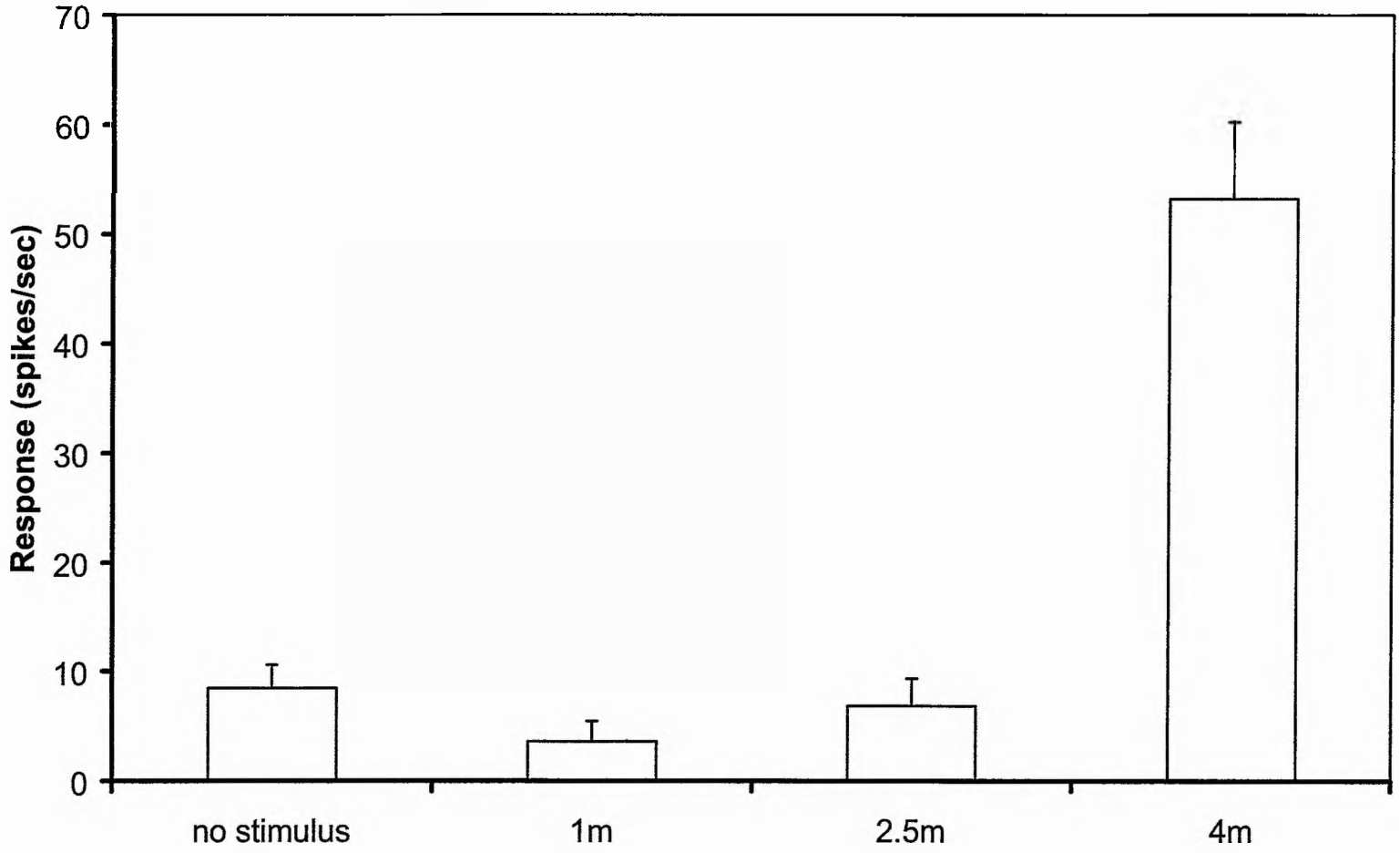


Figure 8.5 Responses of cell T20_2832 to a static human at different distances (One-way ANOVA: $F_{3, 16} = 34.7$, $p < 0.00001$). Post-hoc testing shows that the response at 4m is significantly greater than all other conditions. Each condition, n=5.

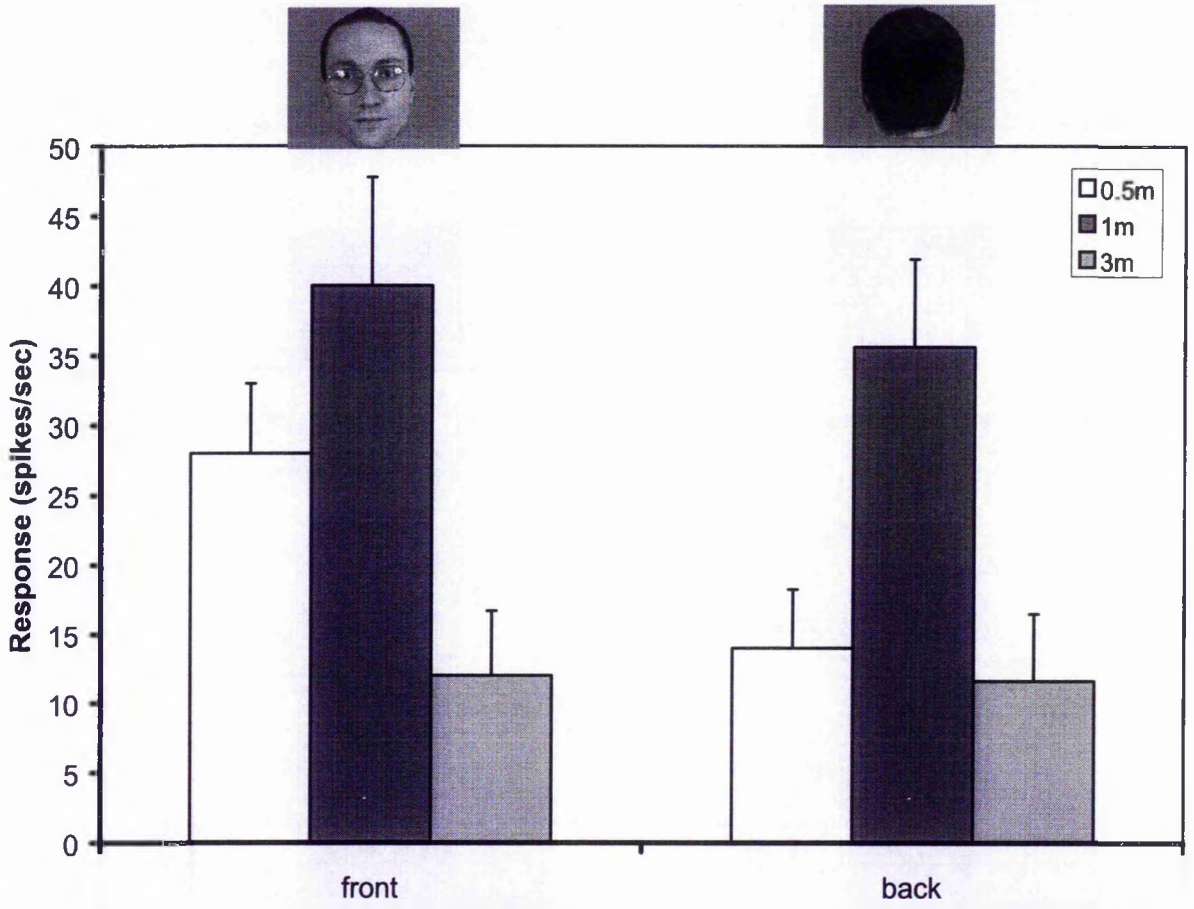


Figure 8.6 Responses of cell S80_2498 to a static human at three different distances either facing the monkey subject or facing in the opposite direction. A two-way ANOVA with view direction and distance as factors shows a significant main effect of distance ($F_{2, 24} = 11.1$, $p < 0.0004$) but no other significant effects. Post-hoc testing shows that the response at 1m is significantly greater than the responses at 0.5m and 3m. Each condition, n=5.

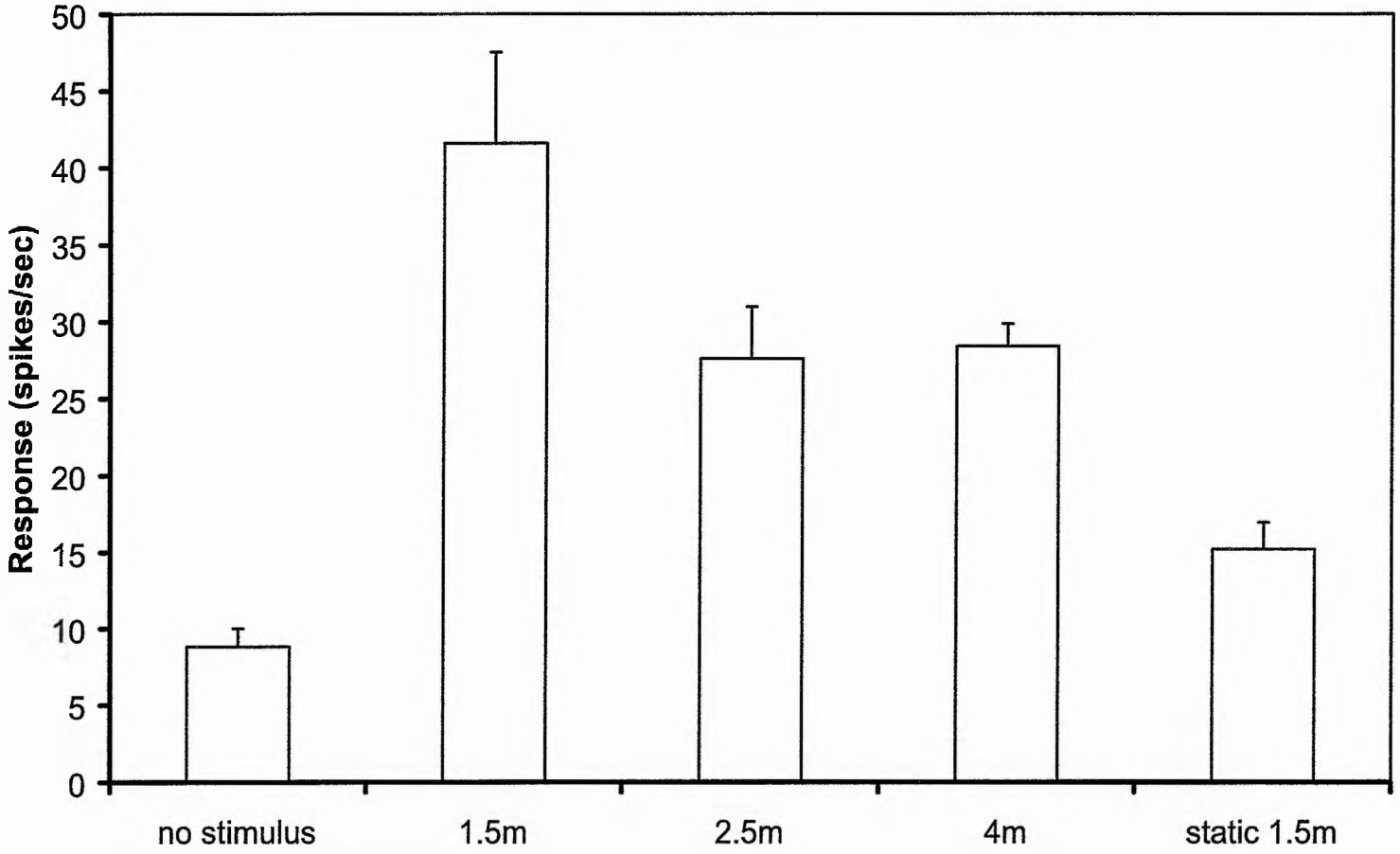


Figure 8.7 Responses of cell T27_3166 to a forward reaching movement made at three different distances (One-way ANOVA: ($F_{4, 20} = 15.3$, $p < 0.00001$). Post-hoc testing shows that the reaching movement elicits a signifucant response at all distances (relative to spontaneous firing) but that the response at 1.5m is significantly greater than the response at 2.5m. The response to reaching at 1.5m is significantly greater than the response to a static person with the arm outstretched. Each condition, n=5.

significance ($p = 0.06$). That reaching movements are required is shown by the response to the experimenter static with the arm out (corresponding to the final state of the stimulus when the reaching movements are made) at the closest distance tested. There is a significant difference between the response to reaching at 1.5m and static at 1.5m, and no difference between static at 1.5m and the cell's spontaneous firing rate.

8.4.3 Lateral position

Although distance effects were the most prominent positional effects observed in the 39 cells under consideration here, 4 cells were found with differential responses to identical stimuli presented at different lateral positions. As with the distance effects described above these differences were observed both for cells responsive to static and for cells responsive to moving stimuli. The cells showing lateral position effects all exhibited different properties and the responses of each cell will be discussed.

The cell illustrated in figure 8.8 was tested with live static human stimuli at four different positions (4m: left right and central; and 1m: central). There is a significant inhibition of activity in response to the experimenter at 1m (relative to spontaneous firing rate). Activity in response to the stimulus presented at all positions 4m away from the subject is significantly greater than activity with the experimenter at 1m from the subject. This is equivalent to the distance effect reported in the earlier cells. For this cell, however, there is also a significant effect of the lateral position of the experimenter with the right position preferred to the central position and the left position. The distance between each lateral position and the

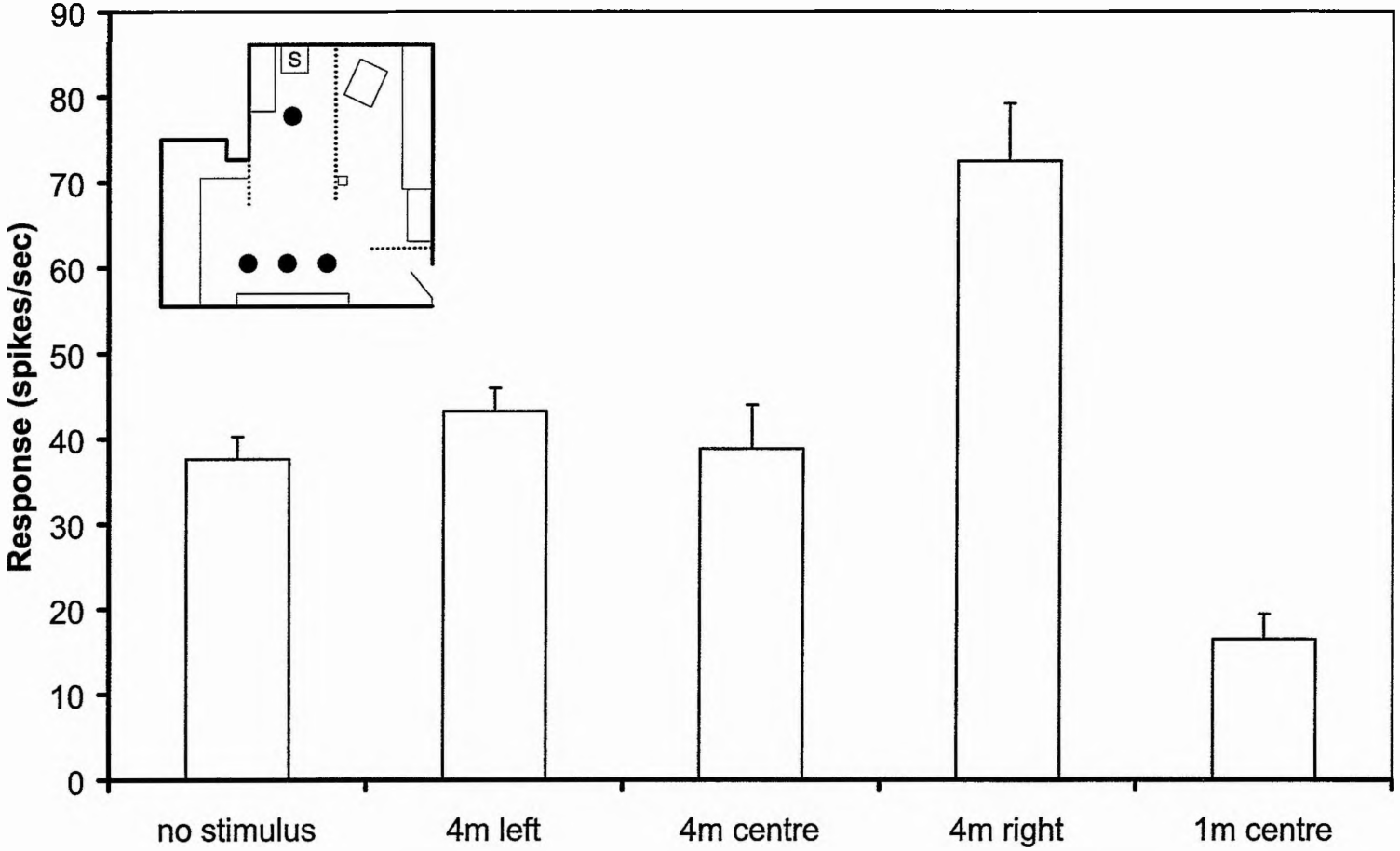


Figure 8.8 Responses of cell T29_2993 to a static human at different positions around the laboratory (One-way ANOVA: $F_{4, 20} = 21.2$, $p < 0.00001$).The figure on the top left of the graph shows a scale plan of the laboratory with the black circles marking the four testing positions (S = subject). Each condition, n=5.

central position was approximately 0.7m. Clinically, the cell seemed to be responding with a "hotspot" on the right side of the laboratory. If an occluder was positioned in front of this position and a person moved behind the occluder, there was no response. Thus, this cell is characteristically different to those reported in chapter 6.

Three of the cells showing lateral position effects exhibited responses related to the entry of stimuli into view and the exit of stimuli from view. The cell illustrated in figure 8.9 showed lateral position effects with slide stimuli. The slides showed a static, profile picture of a person facing left, coming into view from behind an occluder. In two control stimuli, there was either no person, just the background, or the person was completely in view with the same left profile. The cell showed a response to the slide of the person coming into view from behind a central occluder. There was no response (relative to spontaneous firing rate) to a person at the same location but completely in view, or to a slide of a person coming into view from behind an occluder on the right side of the projection screen. Thus there is a significant effect of lateral position and of occlusion.

A different type of lateral position effect is illustrated in figure 8.10. This cell was also tested with slide stimuli. In this case the slides showed a static image of a person exiting from view behind an occluder. There were two different views of the person and for each view the stimuli can be broken down into three different conditions as illustrated in figure 8.10a. For each view the person could be exiting on one side (lateral exit), in the centre (central exit) or could be completely in view. As shown in figure 8.10b, there was a significantly greater response to lateral exit than to central exit with no difference between the two views tested. The cell response

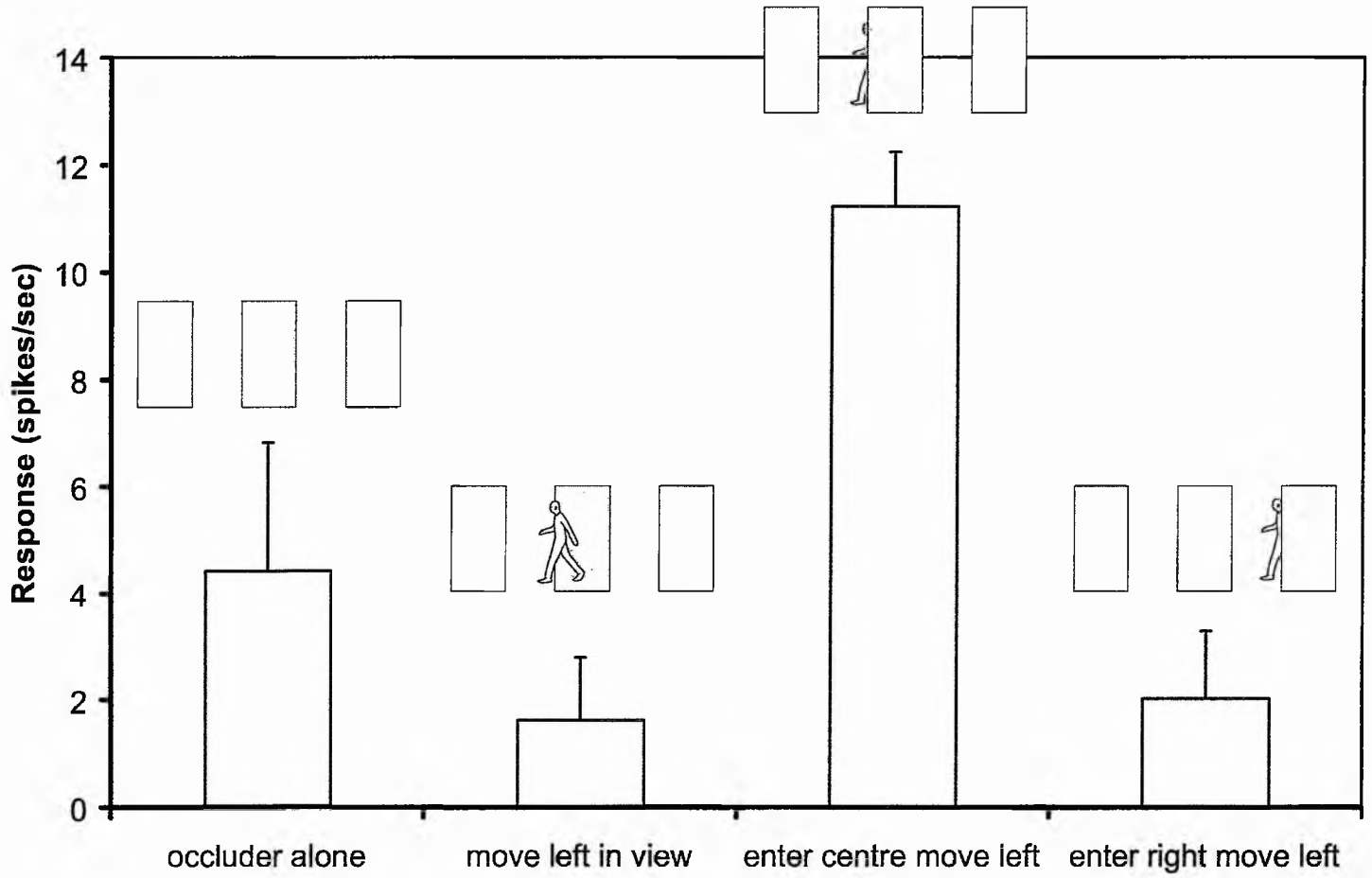


Figure 8.9 Responses of cell S97_2422 to slide stimuli of a person and occluders. One-way ANOVA: ($F_{3, 16} = 8.1$, $p < 0.002$). Each condition, n=5.

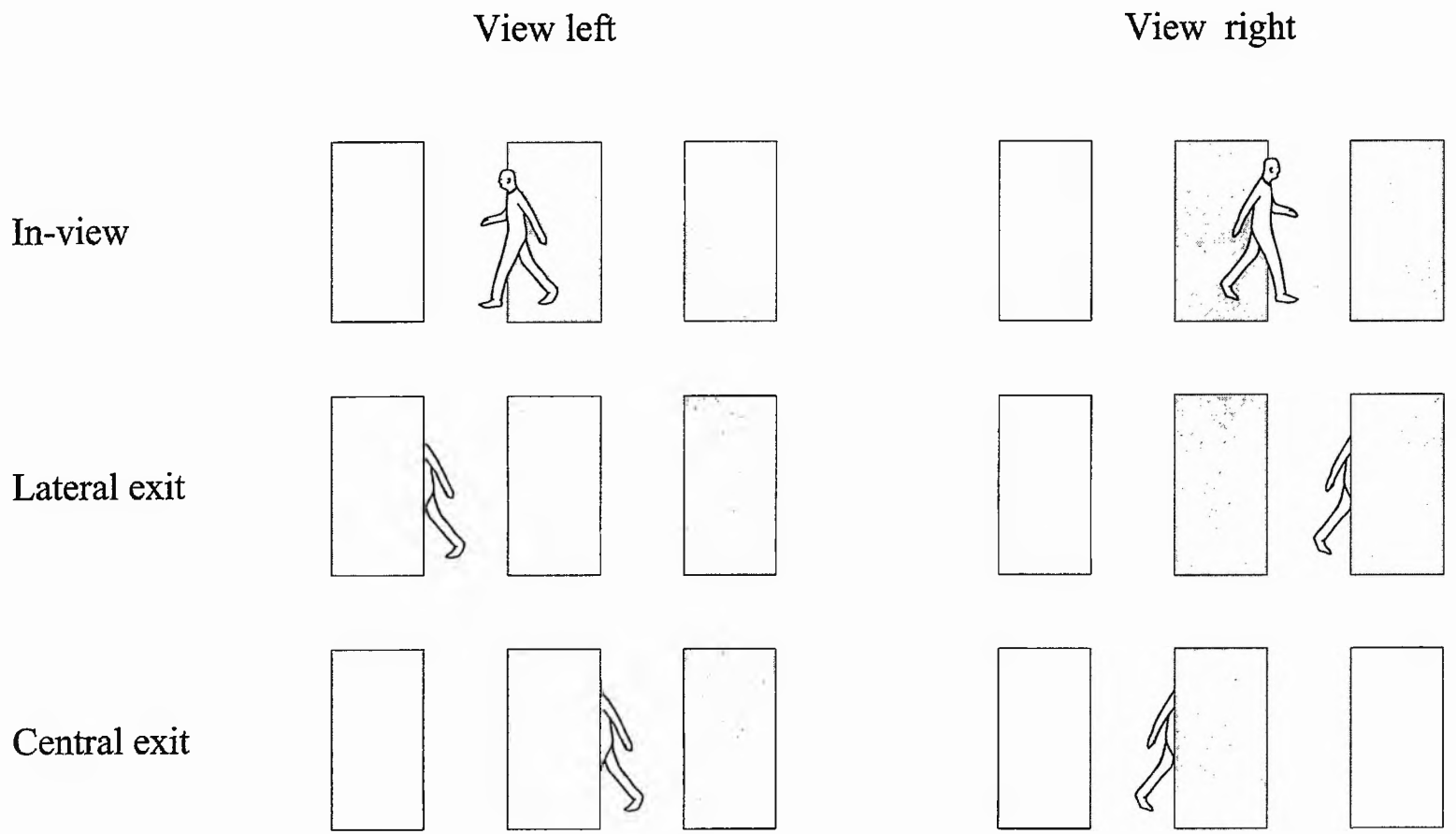


Figure 8.10a Schematic representations of slide stimuli used in testing cell S98_2269.

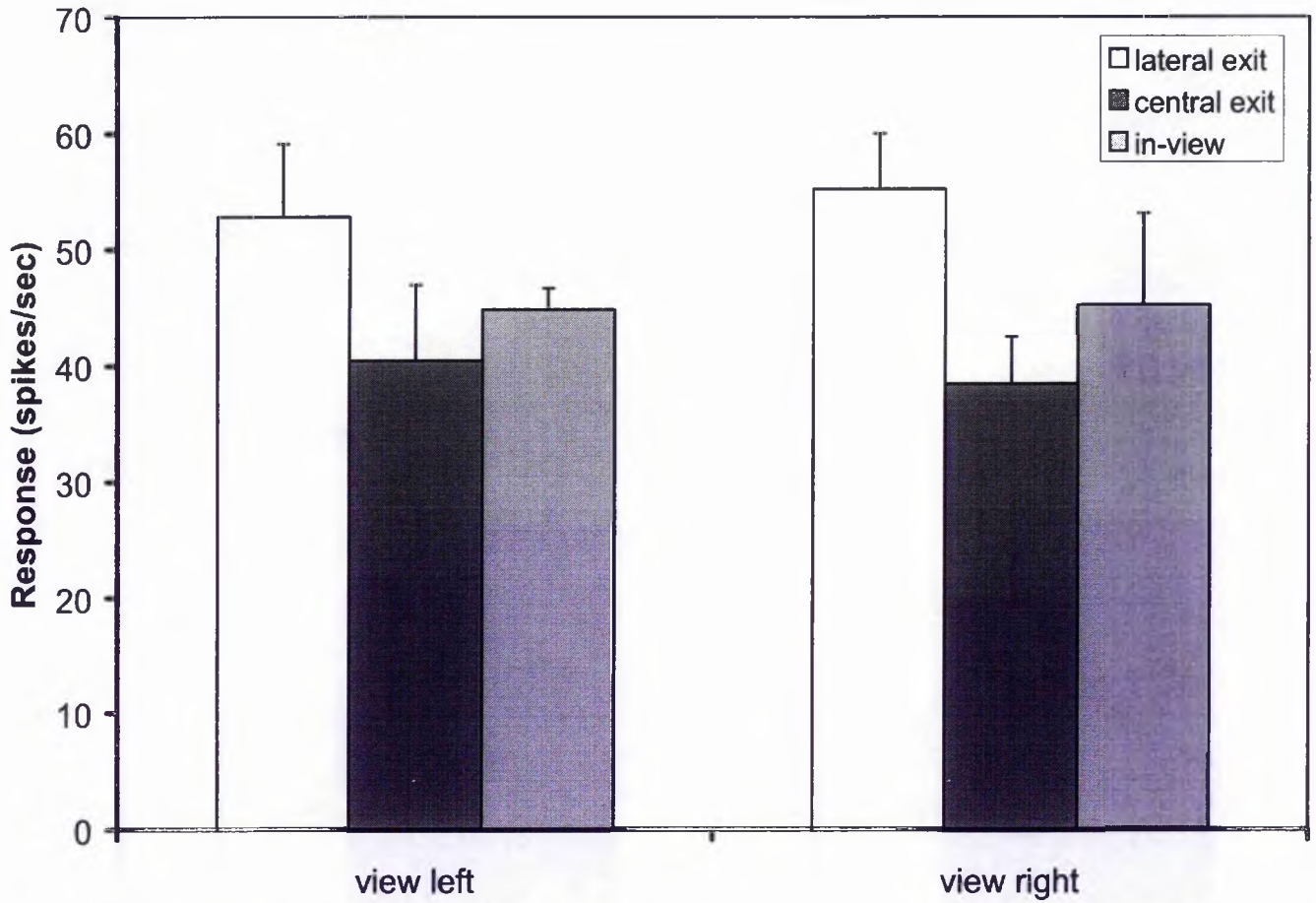


Figure 8.10b Responses of cell S98_2269 to static slide stimuli of a person and occluders. Two-way ANOVA with view and condition (lateral exit, central exit, move-in-view) as factors shows a significant main effect of condition ($F_{2, 24} = 3.5$, $p < 0.05$). Post-hoc testing shows that lateral exit is significantly greater than central exit. Each condition, n=5.

can be described as a preference for people exiting from view at the periphery of the screen.

As with the distance effect described earlier, lateral position effects were observed for cells selective for both static and moving stimuli. The cell illustrated in figure 8.11 responded to the entry of people and objects into view from behind an occluder. Four different positions of entry were tested with two different directions of motion. Responses to entry with the left profile view were significantly greater than responses to entry with the right profile view. For both profile views responses to lateral entry were greater than responses to central entry.

None of the cells described above (figures 8.9, 8.10 and 8.11) with responses related to the occlusion or revealing of stimuli showed the characteristic, long duration changes in activity of the cells described in chapter 6.

8.4.4 Form selectivity

Form selectivity was observed in 14/39 cells described here showing distance or lateral position effects. An example of form selectivity has already been presented in figure 8.9. This cell responded to an image of a part occluded person but not to a person fully in view. Further examples of form selectivity are shown in figures 8.12, 8.13 and 8.15. The cell illustrated in figure 8.12 has already been described (see figure 8.8). This cell showed differential responses depending on the lateral position of a static person. The cell was further tested in its preferred location with different views of a static person. The front view elicited significantly greater responses than the back view (with the response to side views intermediate) and the response to the front view with a twisting movement was significantly greater than all other

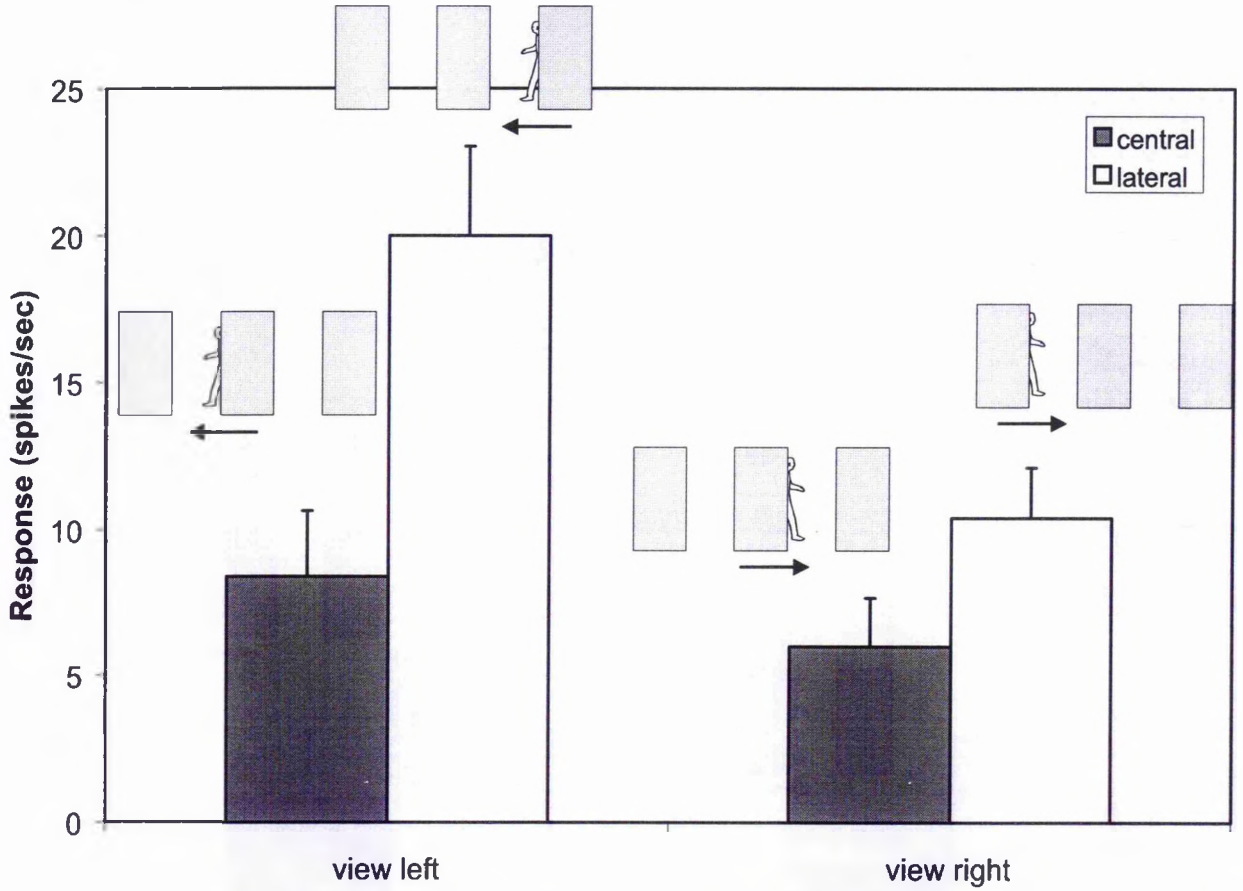


Figure 8.11 Responses of cell S90_2411c to an experimenter coming into view from behind an occluder at different positions within the laboratory. Two-way ANOVA with view and condition (lateral entry or central entry) shows a significant main effect of both view ($F_{1, 16} = 7.2$, $p < 0.02$) and condition ($F_{1, 16} = 12.9$, $p < 0.0025$), but no view by condition interaction. Post-hoc testing shows that left view lateral entry is significantly greater than all other conditions. Each condition, n=5.

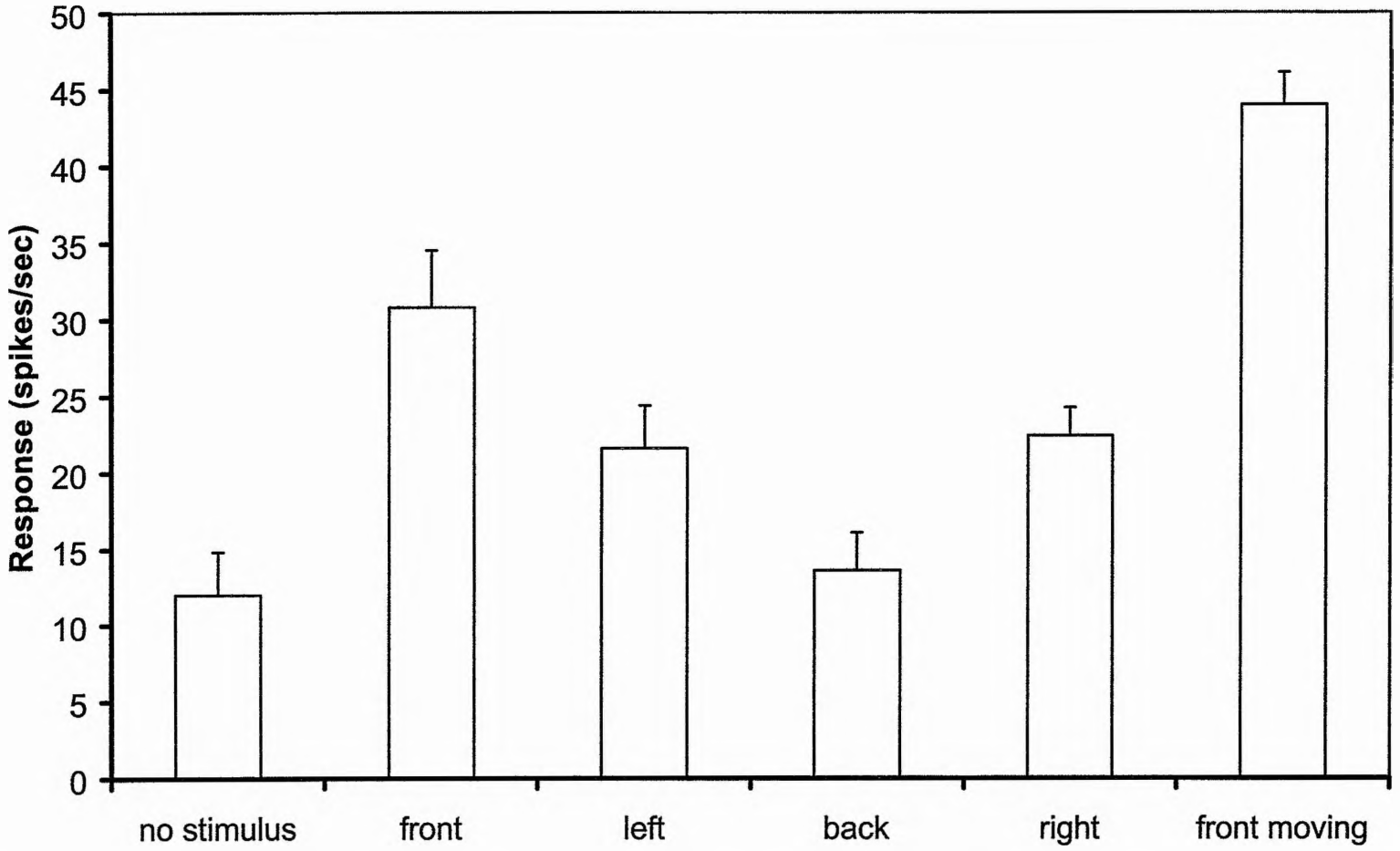


Figure 8.12 Responses of cell T29_2993 to different views and to movement. This cell responded preferentially to stimuli on the right side of the laboratory at a distance of 4m (see figure 8.8) and the stimuli presented here were at the same location (One-way ANOVA: $F_{5, 24} = 19.5$, $p < 0.00001$). Each condition, n=5.

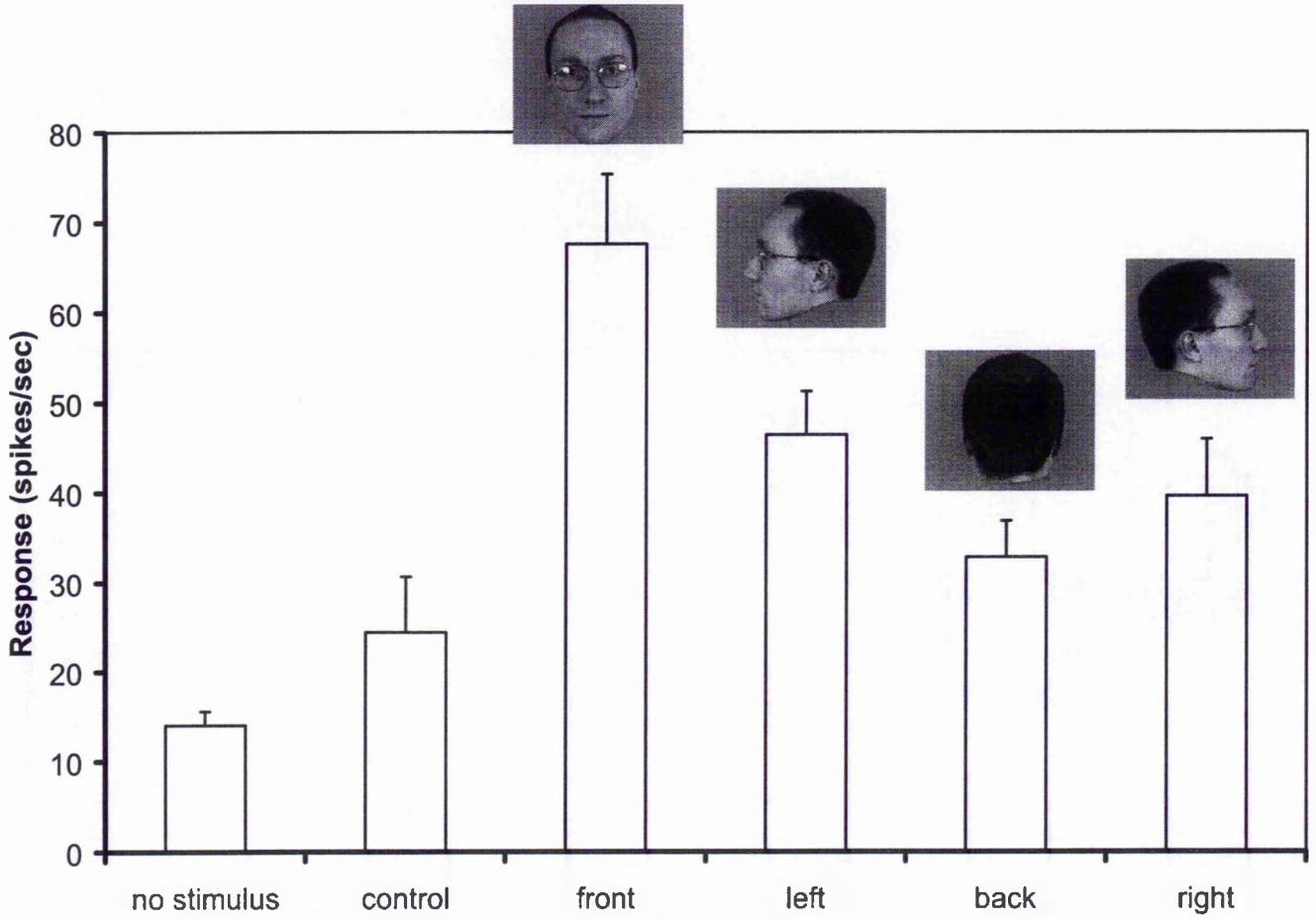


Figure 8.13 Responses of cell T23_3169 to different views of the experimenter presented at a distance of 1m. This cell responded preferentially to stimuli presented at this distance compared with stimulus presentation at greater distances away from the subject (One-way ANOVA: $F_{5, 24} = 11.5$, $p < 0.00001$). Each condition, n=5.

conditions. Similar view sensitivity is illustrated for cell responses in figure 8.13. This cell responded only to stimuli presented very close to the monkey subject (<1m). There were differential responses to the views of the head with the greatest response to the front view.

Form selectivity was not, however, evident in all cells tested. For example, the cell illustrated in figure 8.6 showed equal responses to the front and back views of the head. A further example is shown in figure 8.14. This cell was tested with three different objects (bin, book and head), all varying in size (height 27cm, 30cm and 23cm), at two different distances (0.5m and 1.5m). At the nearest distance the objects subtended 30.2, 33.4, and 25.9 degrees, respectively. For each object there was a greater response when the object was presented at the nearest distance, but there was no difference in the response to the different objects.

Retinal size and distance are conflating factors in much of the testing described so far. As distance from the subject increases the retinal size of the image decreases and vice versa. The distance effects reported here could be interpreted as effects of size. For 5 cells, however, size alone did not seem to be the determining factor. These cells responded preferentially to stimuli presented close to the subject but did not respond to the same degree to images of much larger size presented further away and subtending a similar visual angle. For example, the cell illustrated in figures 8.15 and 8.16 showed greater responses to static human heads presented close rather than far and responded more to a human head than to a mop, of similar size (figure 8.15). This cell was tested with different views of a static human head presented at a distance of 0.7m from the subject and subtending approximately 19 degrees of visual angle, and much larger laserdisc images of views of a head presented at a distance of 4.4m and subtending approximately 21 degrees of visual

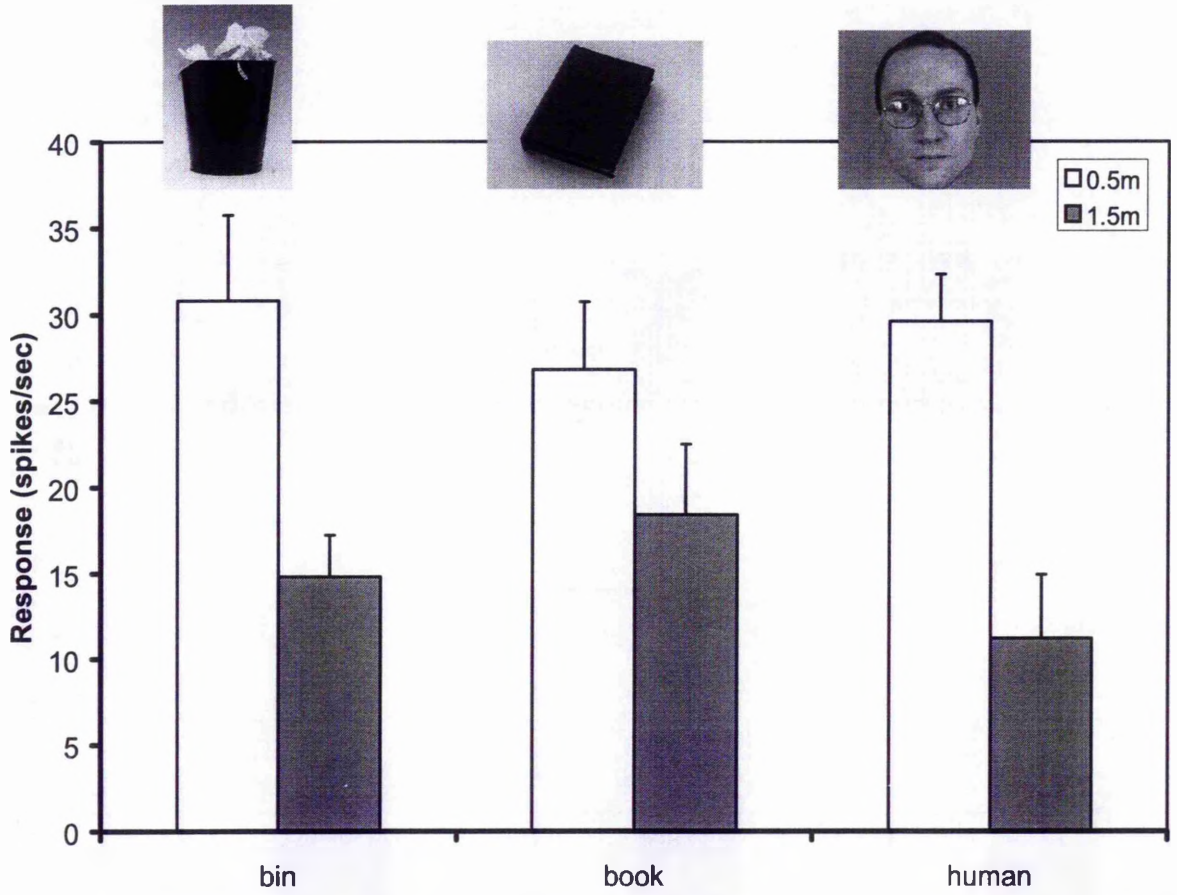


Figure 8.14 Responses of cell S79_2609 to different objects (bin, book and head - heights 27cm, 30cm and 23cm respectively) presented at different distances. Two-way ANOVA with object and distance as factors shows a main effect of distance ($F_{1, 24} = 21.9$, $p < 0.0001$), but no effect of object and no object by distance interaction. The cell shows increased responses for objects presented at 0.5m compared with 1.5m, but exhibits no form selectivity between the different objects. Each condition, n=5.

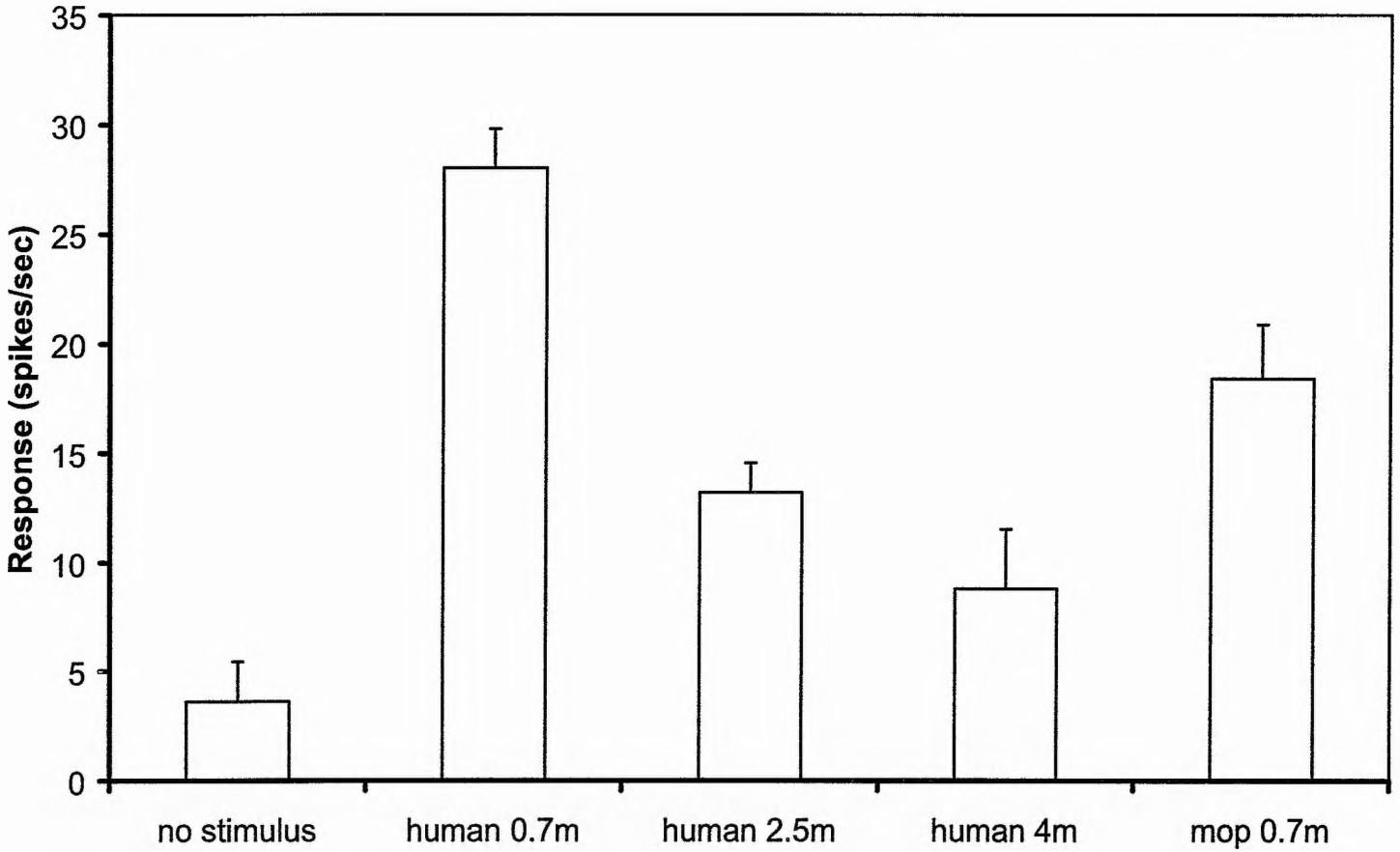


Figure 8.15 Responses of cell T23_3059 to a static human presented at different distances and to a mop presented at the closest distance (One-way ANOVA: $F_{4, 20} = 19.9$, $p < 0.00001$). The cell shows significant responses compared with spontaneous firing levels with the human at 0.7m and 2.5m but not at 4m. There is also a significant response to the mop but this response is less than that to the human at the same distance. Each condition, n=5.

angle (figure 8.16). Thus there is very little difference in retinal image size of the stimuli. The response of the cell was very different, however, with much greater responses to the close head than to the far head of comparable retinal size. Furthermore, the response to the front view laserdisc image (5.6 +/- 2.8 spikes/sec) was very similar to the response to a live human head presented at the same distance (8.8 +/- 2.7 spikes/sec). The cell also showed view selectivity with the greatest responses to the right profile view of the head for both types of stimuli.

8.4.5 Frame of reference

The spatial reference frame of the cells was examined in one of the cells studied. The general properties of this cell have already been described (figures 8.8 and 8.12). The cell showed a preference for stimuli presented at a distance of 4m on the right side of the laboratory. To test the spatial reference frame the monkey was rotated through approximately 45 degrees clockwise. If the cell was responding in an egocentric framework (see chapters 2 and 6) then the spatial responsiveness of the cell should rotate with the monkey. The cell did not respond to stimuli presented at 4m on the left and in the centre of the laboratory. When the monkey is rotated, therefore, if the cell is responding in an egocentric framework, the same spatial location in the room should now be less effective than with the monkey in its normal position. If, however, the cell is responding in an allocentric framework, the responsiveness of the cell should remain in the same spatial location in the room when the monkey is rotated. The results of this test are illustrated in figure 8.17 and it can be seen that there is no difference in response between the two conditions. This

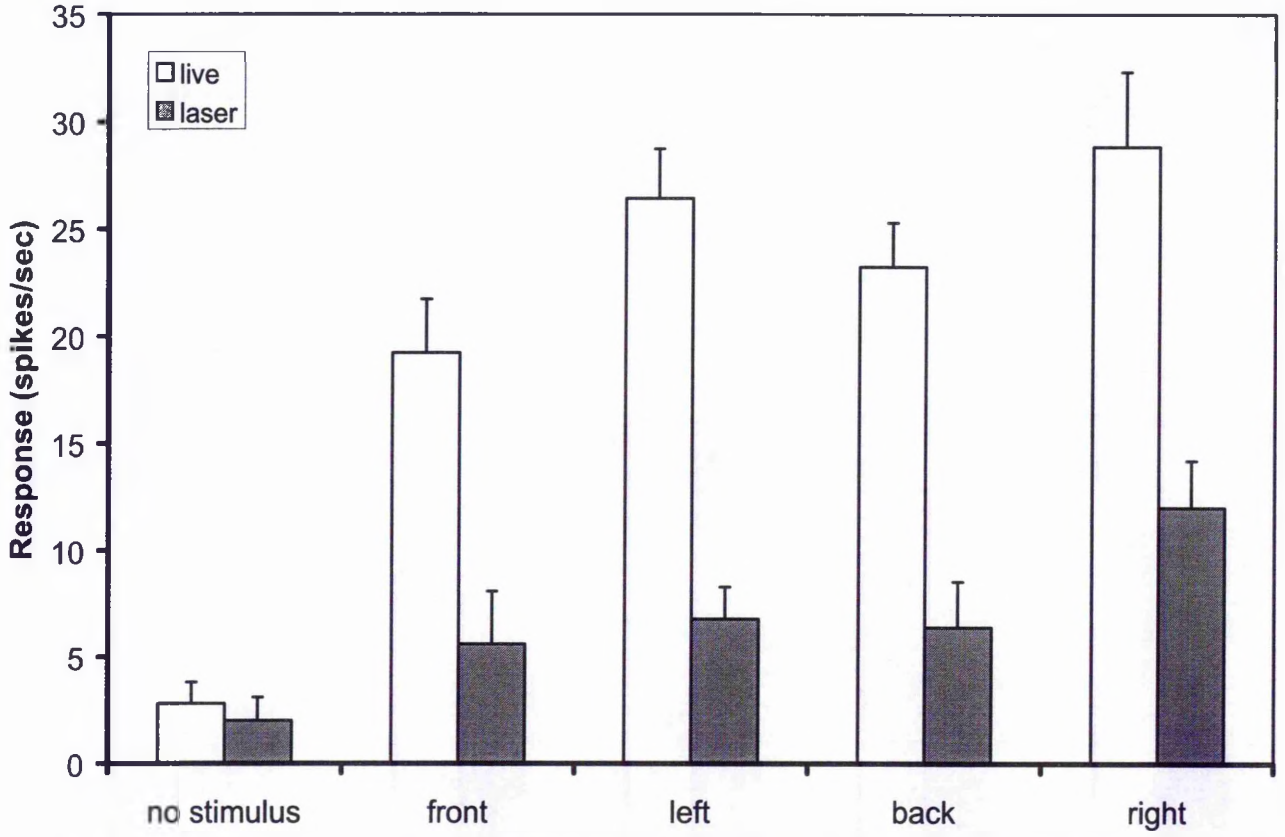


Figure 8.16 Response of cell T23_3059 to different head views presented either live at a distance of 0.7m or from laserdisc at a distance of 4.4m. Two-way ANOVA with view and condition as factors shows a main effect of both view ($F_{4, 40} = 19.0$, $p < 0.00001$) and condition ($F_{1, 40} = 95.0$, $p < 0.00001$) with a significant view by condition interaction ($F_{4, 40} = 5.7$, $p < 0.001$). Post-hoc testing shows that the response to no stimulus is significantly less than all other views, and that the general response to view right is significantly greater than view front. Live presentation is significantly greater than laserdisc presentation for all views except no stimulus. Each condition, n=5.

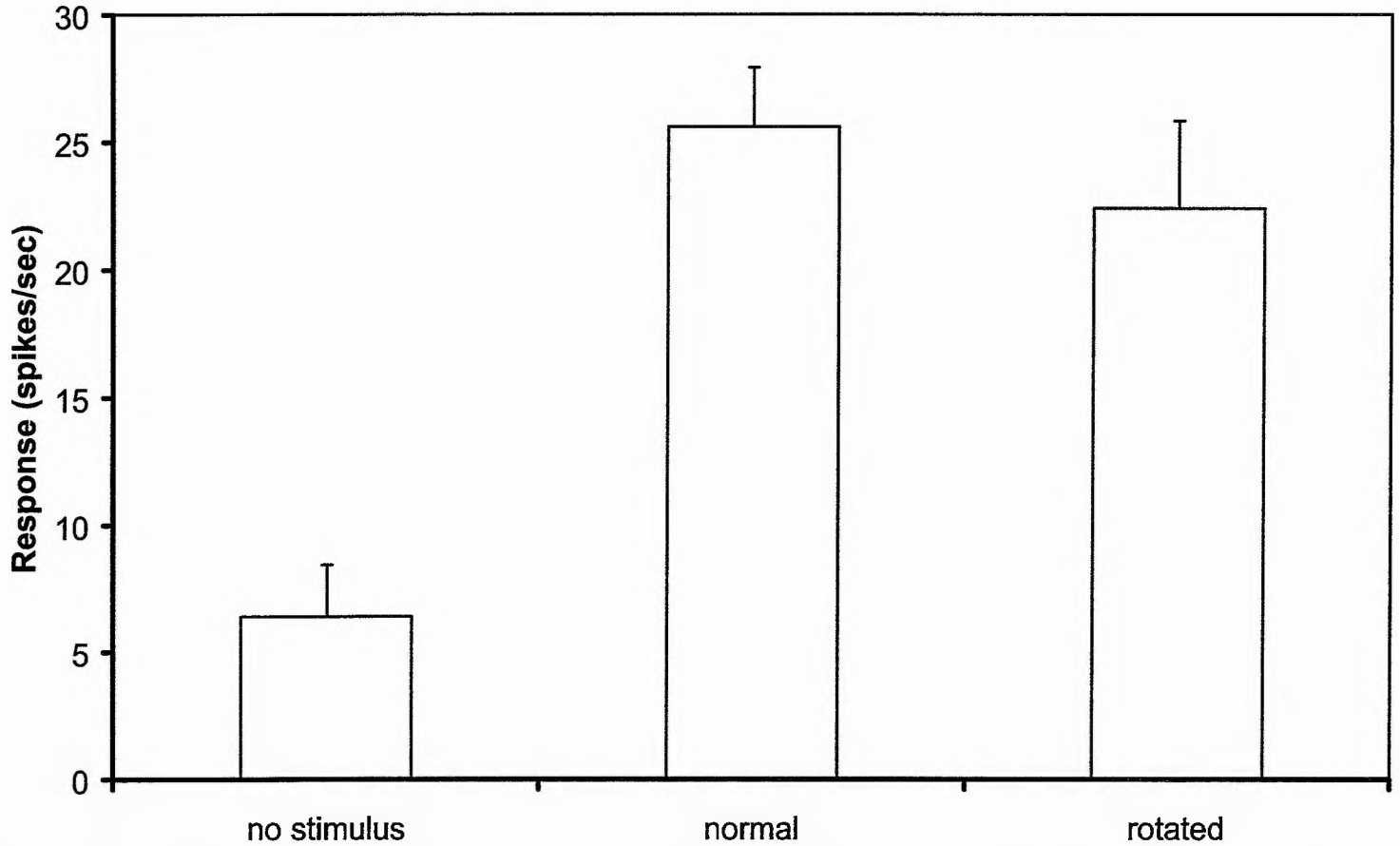


Figure 8.17 Responses of cell T29_2993 to a static human with rotation of the monkey subject 45 degrees. This cell showed a preference for stimuli presented at 4m on the right side of the laboratory. Stimuli presented centrally or on the left were less effective. One-way ANOVA shows a significant effect of conition ($F_{2, 12} = 14.9$, $p < 0.001$), with both conditions of stimulus presentation significantly greater than no stimulus, There is no difference, however, between the normal and rotation conditions. Each condition, n=5.

is suggestive of the allocentric coding of space. For both conditions there is a significant response compared with spontaneous firing levels.

8.4.6 Cell localisation

The x-rays taken at the end of each recording session (see appendix B) show that the cells described in the current chapter are co-extensive with those described in the previous two chapters. This confirms that the cells were located within the superior temporal sulcus.

8.5 Discussion

8.5.1 Summary of results

The cells described in this chapter provide further evidence for spatial sensitivity in areas associated with the ventral stream of cortical visual processing. Cells in STSa were found with differential responses depending on the distance of the stimulus from the subject, and a smaller group of cells showed differential responses depending on the lateral position of the stimulus. This spatial sensitivity was seen in a wide variety of different cell types, suggesting that spatial sensitivity is not limited to a defined subset of cells.

Previous studies in STSa have reported no effect of changing the distance of the stimulus from the subject (Perrett *et al.*, 1982; Perrett *et al.*, 1985) but the range of distances tested was small and the effects were only reported clinically. The lack of effect observed may be dependent on the lack of systematic study.

In a recent study, Dobbins *et al.* (1998) reported distance modulated cell activity in V4 (part of the ventral stream of cortical visual processing). The results reported here show spatial sensitivity in a higher cortical area associated with the ventral stream.

8.5.2 Retinal size and distance

With increasing distance of the stimulus from the subject, the retinal size of the stimulus diminishes, and the effects that have been ascribed as distance effects could be explained as an effect of retinal size. The effect of size on cell responses in temporal cortex has previously been examined. In IT cortex Ito *et al.* (1995), Schwartz *et al.* (1983), Sato *et al.* (1980), Lueschow *et al.*(1994) and Sáry *et al.* (1993) have all reported changes in cell response with changes in size of the visual stimulus. Many of these studies (Lueschow *et al.*, 1994; Sáry *et al.*, 1993; Schwartz *et al.*, 1983) reported size invariance for the majority of cells tested. In these papers size invariance has been defined as constant stimulus shape selectivity despite changes in image size. There are, however, changes in absolute level of cell firing with changes in stimulus size. Changes in stimulus size have often been referred to in terms of octaves where one octave represents a two-fold change (either doubling or halving) in stimulus size. Ito *et al.* (1995) reported that 43% of cells had a size tolerance of less than 2 octaves, 36% a tolerance of between 2 and 4 octaves and the remaining 21% a size tolerance of greater than 4 octaves. All the other studies in IT cortex have only examined changes in stimulus size of 2 octaves or less, much less than stimulus changes that are likely to be observed in the natural environment.

All of the studies in IT cortex used arbitrary stimuli which do not have an expected absolute size. In STS, studies on size have used more complex stimuli, often human or monkey faces or bodies that have expected absolute sizes based on previous experience. Perrett *et al.* (1982) varied the retinal size of human head stimuli by changing the distance of the stimulus from the subject. They found no change in cell responses to stimuli presented at distances of between 0.2 and 2m, representing a ten-fold decrease in stimulus size. Conflicting results on size have been reported in more quantitative studies by Rolls and Baylis (1986) and Ashbridge and colleagues (Ashbridge *et al.* 1998; Ashbridge and Perrett, 1998). Rolls and Baylis (1986) reported a range of different responses to varying stimulus size with some cells showing no change in response across different sizes, and some cells responding across a range of sizes with responses diminishing with either very large or very small stimuli. They reported that 95% of neurones tolerated a 4x change in size, corresponding to 2 octaves. Distance of the stimuli from the subject was found to have little effect and when it did, the effect could be compensated by a change in retinal size. For example, if the response of a cell declined with increasing distance, increasing the retinal size of the image could reverse this. There was an apparent trade-off between retinal size and distance, suggesting an importance of retinal image size over distance. For a small group (n=4) of neurones absolute size was found to be important and there was no effect of distance. These cells gave equivalent responses to a stimulus presented at different distances despite changes in retinal image size (see also Perrett *et al.*, 1982; Perrett *et al.*, 1985).

In contrast, Ashbridge and colleagues (Ashbridge *et al.* 1998; Ashbridge and Perrett, 1998) found that the vast majority of cells tested in STSa were sensitive to the size of the stimulus. The stimuli presented were human figures at a distance of

4m, and size was systematically varied with maintained distance. They found that 75% of cells only tolerated a size change of less than one octave and that the majority of the cells tested responded preferentially to life-sized or near life-sized stimuli. In this study, however, stimuli were never greater than life-size.

In the current study, the changes in distance correspond to size changes of between 2 and 3 octaves although differential responses were observed for distances corresponding to size changes of less than 2 octaves (e.g. see figure 8.3). Ashbridge and colleagues (Ashbridge and Perrett, 1998; Ashbridge *et al.*, 1998) but not Rolls and Baylis (1986) reported differential responses to size across similar octave changes. Size, however, cannot explain at least some of the effects observed. In contrast to Rolls and Baylis (1986), changing retinal size did not reverse the effects of distance in those cells tested (e.g. see figure 8.16), suggesting that retinal size alone cannot explain the responses. Such testing compared 3-D stimuli of one image size with 2-D images of equivalent retinal size but at an increased distance. Lack of response at an increased distance might reflect lack of response to 2-D stimuli, rather than a lack of response to the increased testing distance. Selectivity for 3-D stimuli has been reported amongst STSa cells responsive to faces but is, however, relatively rare (Perrett *et al.*, 1984; Rolls and Baylis, 1986).

For familiar objects, such as the stimuli used in the experiments described here, retinal size of the image can provide information about the distance of the stimulus from the subject. Size and distance cannot be considered in isolation. Ashbridge and colleagues (Ashbridge and Perrett, 1998; Ashbridge *et al.*, 1998) found that the majority of cells were tuned to life-sized images. All stimuli were presented at the same distance and it is not known if the cells would respond to equivalent absolute-size images at a different distance or whether the selectivity for

life-size images would remain. Rolls and Baylis (1986) reported some cells that responded to the absolute size of images regardless of distance, but the majority of cells they reported showed generalisation across size. In the current study, most stimuli were presented at life-size at different distances. In the cells tested, retinal size was not found to be critical. Therefore, if the cells described here are equivalent to the cells described by Ashbridge and colleagues in an overlapping area of STSa (Ashbridge and Perrett, 1998; Ashbridge *et al.*, 1998) it would imply that there are cells tuned to particular sizes at particular distances.

8.5.3 Stimulus change with distance

As the distance of the stimulus from the subject varies there is also some change in the image of the stimulus itself. At distances very close to the subject, parts of the stimulus are occluded by the shutter box and other parts of the primate chair. At the shortest distance, with human stimuli, the head only is visible. At greater distances parts of the body become visible as well. It is possible that such changes could account for some of the effects observed with distance. Cells in STSa (Wachsmuth *et al.*, 1994; Wachsmuth, 1995) have been described with differential responses to different body parts presented both static and in motion. Cells were tested with views of the whole body, the body alone (head occluded) or the head alone (body occluded). Some cells responded to the view of the whole body, but not to the head or body in isolation. Other cells responded to the whole body and the body alone but not the head. One cell showed a greater response to the head alone than to the whole body or body alone (Wachsmuth, 1995). In the current study, however, the whole body and head was in view with distances greater than 2.4m

from the subject. Differential effects of body parts, therefore, cannot explain differential responses between distances greater than 2.4m (e.g. figures 8.3 and 8.5). Furthermore, differential effects of body parts cannot explain the lateral distance effects reported in four of the cells studied here.

Although there was inevitably some change in the stimulus with distance, differential effects of body parts cannot explain all of the responses observed in the current study.

8.5.4 Anatomical considerations

Anterior regions of the STS receive connections from parietal cortex (e.g. Baizer *et al.*, 1991, Seltzer and Pandya, 1984), posterior regions of STS including the motion areas MST and FST which are heavily connected with area MT (Boussaoud *et al.*, 1990) and from parahippocampal cortex (Seltzer and Pandya, 1994) and entorhinal cortex (Good and Morrison, 1995). Any or all of these connections could provide the spatial input required to account for the positional effects described in this thesis. On the basis of anatomy alone, STSa has been described as a site of integration of spatial and object information (Baizer *et al.*, 1991) and may represent a third stream of cortical visual processing (Boussaoud *et al.*, 1990). A recent connectional analysis of cortical visual areas (Jouve *et al.*, 1998) has suggested a strong link between STS and area TH of the parahippocampal cortex, an area that has been implicated in many of the studies of spatial function in the ventral brain (see section 8.1). The recent finding (Dobbins *et al.*, 1998) of distance sensitivity in area V4, however, suggests that position may be coded throughout the ventral stream and the properties described here could also be derived

from processing within the ventral stream rather than the inputs from outside the ventral stream as described above.

8.5.5 Objects and space

The original distinction of separate streams in cortical visual processing (Ungerleider and Mishkin, 1982) described a "what" and a "where" system. Emphasising the ouputs of the visual system, Milner and Goodale (Goodale and Milner, 1992; Milner and Goodale, 1993, 1995) proposed that a more appropriate distinction is "what" and "how" and argued that spatial information may be important in both visual streams. Information in the dorsal stream appears to be coded in egocentric frameworks (see chapter 2) and it may be that spatial information in the ventral stream is coded in allocentric terms (e.g. Dijkerman *et al.*, 1998). Farrell (1996) has suggested that topographical disorientation results from damage to an allocentric coding system located in the ventral stream.

Cells within anterior regions of the superior temporal sulcus show responses to socially relevant stimuli such as faces and bodies and may process gaze direction, a highly important social cue. The STS along with the lateral basal nucleus of the amygdala has been proposed as a crucial site for the coding of the social behaviour of macaques (Emery, 1997). Determining the direction of attention of another individual may require spatial information (Harries and Perrett, 1991). In coding whether or not a conspecific is directing attention at you, egocentric spatial information may be sufficient. The spatial relationship of the conspecific to you is critically important. In coding the direction of attention when that attention is directed at a position or another conspecific may require allocentric information. The

relative positions of the object of attention and the attending individual are now important. Such a relationship between two visible items is more likely to be coded in an allocentric framework (see Dijkerman *et al.*, 1998). The positions could be coded in an egocentric framework, but if future behaviour is to be directed to the position or object of attention, then an allocentric framework is more useful.

The cells with positional sensitivity in STS that were tested showed allocentric coding of spatial information. This suggests that STSa may be developing an allocentric code for object position or may be receiving allocentric position influences from areas of the hippocampal formation.

8.5.6 Lack of positional sensitivity in previous studies

The question arises as to why previous studies have not observed the spatial sensitivity of cells in temporal cortex. Given the predominant view of the dorsal and ventral streams in cortical visual processing most studies have concentrated on investigating object processing in the ventral stream. A similar bias has dominated study of the dorsal stream with studies concentrating on spatial perception, but Sereno and Maunsell (1998) recently recorded from neurones in the lateral intraparietal area and found sensitivity to visual form in fixation tasks in which there was no behavioural requirement connected with the visual stimuli presented. Adoption of the spatial tasks commonly used in analysis of the dorsal stream to study the ventral stream may reveal spatial sensitivity in an area thought to be unaffected by spatial position.

Many of the spatial tasks that have been used in studies of spatial processing are tasks that can be solved in egocentric co-ordinate systems and may rely heavily

on the dorsal stream. In tasks requiring the use of allocentric spatial information, the importance of the ventral stream may be highlighted.

In functional imaging studies the test and the control conditions may equally involve the areas of the ventral stream. When the conditions are subtracted to reveal areas of activity associated with the test task, activity associated with object position in temporal cortical areas may be lost. Such arguments have been used to account for the absence of hippocampal activity observed in many spatial tasks (e.g. see section 8.1.4).

8.6 Summary

There is much evidence to show the involvement of ventral brain areas in spatial processing. The hippocampus has been the focus of much research into spatial abilities, but it is now evident that areas outside the hippocampus are critical for spatial processing. These areas include the parahippocampal cortex and entorhinal cortex, but the evidence suggests that there may also be an involvement of temporal neocortical areas. These areas are intimately connected with parahippocampal and entorhinal cortex. The cells described in this chapter provide further neurophysiological evidence for spatial processing within the anterior superior temporal sulcus, confirming anatomical evidence that this area is a site for the integration of object and spatial information. Such integration may reflect the importance of spatial position in the analysis of social signals.

CHAPTER 9

GENERAL DISCUSSION

9.1 SUMMARY OF FINDINGS

The experiments described in this thesis have demonstrated that:

(a) Macaques maintain a representation of the motivational value and form of objects that are out of sight. This is reflected in behavioural measures of the retrieval of hidden objects.

(b) Cells in STSa code the presence and location of objects that are out of sight and may therefore contribute to object permanence.

(c) Cells in STSa exhibit auditory-visual interactions that may help in the binding of auditory and visual information.

(d) There is coding of position in STSa, confirming anatomical suggestions that this area may be a site for the integration of spatial and object information.

Object permanence has been extensively studied at a behavioural level in both humans and non-humans. At a basic level object permanence relates to the continued existence of objects that are out of sight. Search for a hidden object is taken as evidence for object permanence, but tells nothing about the nature of the representations of those occluded objects. In lower animals such search can arise from the adoption of stereotyped movements following occlusion (e.g. invertebrates)

or from simple association of events (if A then B, e.g. chick). Representations of the occluded objects are not required. Inherent in the concept of object permanence are assumptions about the spatial and physical properties of the occluded object and the continued dependence on physical laws. A number of studies suggest that monkeys fail to reach the highest levels of object permanence and are unable to represent the unseen movements of hidden objects, although such a conclusion remains controversial. The behavioural study described in this thesis has quantitatively replicated previous findings suggesting that macaques maintain a representation of the motivational value of food rewards that are out of sight. Furthermore, measures of the retrieval of the food reward suggested that macaques might also maintain a representation of the form of the reward. Unseen changes in the nature of the reward may disrupt any pre-planned motor strategies, leading to more errors and increased time taken in picking up an unexpected versus an expected reward object.

Although extensively studied at a behavioural level little is known about the neural mechanisms of object permanence. Phenomenological studies have stressed the importance of the visual configuration of natural occlusion in generating expectations about maintained existence. In previous studies of STSa of macaques, cells have been found that respond transiently to the exit of stimuli from view. Such studies, however, presented stimuli over a short duration and failed to examine the reappearance of stimuli. A separate population of STSa cells was found, however, to respond transiently to the entry of stimuli into view. In the neurophysiological study presented here, the responses of neurones in the anterior STS were recorded while objects moved out of sight and came back into view following a period of complete occlusion lasting between 3 and 20 seconds. A population of neurones was found to respond, often maximally, during the period of occlusion. The manner of occlusion

was found to be critical with the majority of cells tested responding only if there was gradual occlusion of the stimulus. Sudden disappearance of the stimulus (produced by closing an LCD shutter) failed to elicit activity. This visual sensitivity to the configuration of occlusion echoes the importance that many psychologists (e.g. Michotte, 1950, 1955) gave to visual events (e.g. gradual occlusion) in establishing object permanence.

To search for a hidden object requires not only knowledge of the nature of the hidden object, but also knowledge of the position of the object. Consistent with a role in object permanence, the population of cells described here showed selectivity for the position of the occlusion within the laboratory. Such selectivity may derive from both the direction of movement prior to occlusion and the position of the occlusion independent of the direction of approach.

Although anatomical studies have suggested STSa to be a site of reconvergence of the dorsal and ventral streams of cortical visual processing, the evidence presented in this thesis is the first reported for coding of position in this area and indeed in temporal neocortex. The positional sensitivity could derive from parietal cortex (i.e. from the dorsal stream) or the hippocampus via the parahippocampal gyrus (parahippocampal cortex and entorhinal cortex).

One view of the streams of cortical visual processing suggests that they represent a functional division between visuomotor processing and object/scene recognition. In contrast to the "what" and "where" dichotomy, such a division implies that both spatial and form information may be coded in the two streams, but for different functions. This is supported by evidence for the coding of form in the parietal cortex during reaching, grasping and simple fixation. The results described here are consistent with this view of the cortical visual streams.

The anterior STS is a polymodal region and cells with auditory responsiveness were found to be modulated by visual stimuli. For some cells auditory responsiveness was increased if the object producing the sound was out of sight. For other cells, the converse was found to be the case. These cells may contribute to the "binding" of auditory and visual stimuli and help in maintaining an awareness of the continued existence of objects hidden from view.

An examination of all cells recorded over the past three years has revealed further evidence for the coding of position within STSa. The predominant effect was that of distance, with some cells responding preferentially to stimuli presented near to the subject and others responding preferentially to more distant stimulation. For a small group of cells the lateral position of a stimulus was found to be important. These positional effects were found in a wide variety of different cell types, suggesting that positional sensitivity does not represent the properties of a small subset of cells in STSa.

The frame of reference for spatial coding was examined in a small number of cells and found to be allocentric. When the monkey was moved the area of spatial sensitivity remained at the same location within the room, and did not move with the monkey. Such a finding is consistent with the view that the ventral stream of cortical processing may be predominantly involved in processing allocentric spatial information. Previous findings of goal-centred and object-centred coding in cells of STSa may be interpreted as reflecting the operation of an allocentric framework. Many cells in STSa, however, show viewer-centred representations (an egocentric representation) and it is likely that the egocentric coding of space may also be found in this area.

It has been suggested that STSa is critically important in social cognition (Emery, 1997). In processing social signals, spatial information may be required to determine the focus of a gesture such as threat. Behaviourally, it is important to determine if a social signal is directed at you or someone else so that appropriate responses can be made. Determination of the direction of attention is required and may involve the use of cues derived from head and eye position and orientation. Distance information may be required to establish the direction of attention and, for example, dissociate a threat directed at you from a threat directed at a conspecific in front or behind you. Such processing could operate on an egocentric spatial framework. Determining whether attention is directed at you or not, however, is only one aspect of social cognition. Determining the focus of attention that is not directed at you may also be important for appreciating dominance hierarchies and areas or objects of interest that may warrant future exploration. Such processing may require an allocentric spatial framework because it is the relative positions of objects that are important and not the position of objects with respect to the observer.

Furthermore, an awareness of the position of conspecifics even when out of sight may be important in interpreting social signals. In the troop situation many individuals will be out of sight and to make sense of the numerous social signals an awareness of their location is important. The presence of an object of attention may make the direction of attention easier to determine even if that object is out of sight. For example, knowledge that a conspecific is behind you may help dissociate a threat directed at you from a threat directed at them.

9.2 Future work

The data presented in this thesis suggests the processing of spatial information in STSa. Such spatial processing in temporal neocortex may not be confined to this area and a more systematic exploration of position sensitivity will reveal the extent of such coding. Most studies have concentrated on the visual recognition aspects of cells in these areas, and effects of position have not been explored. A similar bias has been present in studies of the parietal cortex with most studies concentrating on spatial aspects of cells. A recent study in the lateral intraparietal area (Sereno and Maunsell, 1998), however, has shown form selectivity in a simple fixation task.

In the studies reported here and in previous studies in STSa the framework of both spatial and object representation was not thoroughly examined and a more systematic study is warranted. In particular, moving the position of the monkey relative to the stimulus will help distinguish between ego- and allo-centric coding.

Despite the extensive anatomical and neurophysiological evidence for multisensory coding in STP, this has been a neglected area of research. The data presented in this thesis suggest the presence of high-level auditory-visual interactions and such effects demand more systematic investigation. In the natural environment rarely are unimodal stimuli presented in isolation, and examination of cross-modal effects will be critical in understanding the neural mechanisms of perception.

With greater emphasis on natural stimuli and behaviourally relevant situations, more complexity of coding properties has become evident in high-level visual association cortex. In turn, these properties support an understanding of how subtle cognitive constructs are processed in the nervous system.

APPENDIX A

BEHAVIOURAL DATA

The table on the following pages shows the raw data from the analysis of reaching behaviour of the monkey subject, Steve. The trials are listed in the order of presentation. For each trial the nature of reward is indicated along with the relevant timing and observational measures.

Each trial is listed as either a change (c) or no-change (n) trial and the motivational value of the rewards (V) is given as either high (h) or low (l). The times are listed in the format of the frame counter - "hours: minutes: seconds. frames" - and all timing differences are given in terms of number of frames. For analysis of shaking each trial was broken down into 5 time periods: "ITI" = inter-trial interval, either immediately preceding (before baiting) or following (after closure of trapdoor) a trial; "before" = after baiting well, but prior to reaching; "during" = during reach; "after" = following knocking down of the screen.

STEVE - REACHING:

				Reward		Changed to...		Movements		Pick-up	Drop			Chair Shake					Timings			Timing differences		
Block	No.	TD open	Type	Item	V	Item	V	Prep.	Reach	Clean	Far	Mid	Near	ITI	Before	During	After	ITI	Screen	Past TD	Mouth (first)	Reaction	Retrieval	Withdrawal
1	1	00:00:17.11	n	apple	l			Yes	Yes										00:00:18.05	00:00:19.13	00:00:19.21	19	33	8
1	2	00:00:34.02	n	apple	l			No	No								Yes							
1	3	00:01:03.24	n	smartie	h			No	Yes										00:01:04.19	00:01:06.10	00:01:06.16	20	41	6
1	4	00:01:31.09	n	smartie	h			Yes	Yes										00:01:32.01	00:01:33.12	00:01:33.24	17	36	12
1	5	00:01:50.15	n	smartie	h			Yes	Yes										00:01:51.08	00:01:53.10	00:01:53.18	18	52	8
1	6	00:02:10.20	n	black grape	h			Yes	Yes										00:02:11.13	00:02:12.21	00:02:13.04	18	33	8
1	7	00:02:42.20	c	smartie	h	nothing	l	Yes	Yes										00:02:43.12	00:02:47.22		17	110	
1	8	00:03:10.15	n	smartie	h			Yes	Yes										00:03:11.07	00:03:13.07	00:03:13.17	17	50	10
1	9	00:03:32.22	n	malteser	h			Yes	Yes	Yes									00:03:33.14	00:03:34.14	00:03:34.21	17	25	7
1	10	00:03:51.22	n	smartie	h			Yes	Yes										00:03:52.14	00:03:54.05	00:03:56.00	17	41	45
1	11	00:04:17.13	n	carrot	l			Yes	Yes										00:04:18.04	00:04:24.10	00:04:24.20	16	156	10
1	12	00:04:46.13	n	cabbage	l			Yes	Yes										00:04:47.04	00:04:49.17	00:04:49.22	16	63	5
1	13	00:05:08.15	n	apple	l			No	No															
1	14	00:05:38.06	n	banana	h			Yes	Yes	Yes									00:05:38.20	00:05:39.18	00:05:39.22	14	23	4
1	15	00:05:59.00	n	smartie	h			Yes	Yes										00:05:59.17	00:06:01.18	00:06:02.04	17	51	11
1	16	00:06:27.09	n	black grape	h			Yes	Yes	Yes			Yes						00:06:28.00	00:06:28.19	00:06:29.00	16	19	6
1	17	00:07:03.05	c	smartie	h	black grape	h	Yes	Yes										00:07:04.12	00:07:06.05	00:07:06.13	32	43	8
1	18	00:07:32.11	n	black grape	h			Yes	Yes	Yes									00:07:33.04	00:07:33.22	00:07:34.03	18	18	6
1	19	00:08:12.22	n	smartie	h			Yes	Yes										00:08:13.12	00:08:17.07	00:08:17.14	15	95	7
1	20	00:08:32.19	n	black grape	h			Yes	Yes										00:08:33.10	00:08:35.01	00:08:35.07	16	41	6
1	21	00:08:49.13	n	banana	h			Yes	Yes	Yes									00:08:50.05	00:08:51.01	00:08:51.08	17	21	7
1	22	00:09:11.09	n	malteser	h			Yes	Yes	Yes									00:09:12.00	00:09:12.23	00:09:13.03	16	23	5
1	23	00:09:36.12	n	black grape	h			Yes	Yes	Yes			Yes						00:09:37.03	00:09:37.22	00:09:38.03	16	19	6
1	24	00:10:04.03	n	smartie	h			Yes	Yes										00:10:04.19	00:10:08.19	00:10:08.23	16	100	4
1	25	00:10:22.14	n	black grape	h			Yes	Yes										00:10:23.07	00:10:24.08	00:10:24.17	18	26	9
1	26	00:10:45.24	c	black grape	h	carrot	l	Yes	Yes	Yes		Yes							00:10:46.18	00:10:48.05		19	37	
1	27	00:11:15.13	n	banana	h			Yes	Yes	Yes									00:11:16.06	00:11:18.07	00:11:18.11	18	51	4
1	28	00:11:33.18	n	black grape	h			Yes	Yes	Yes									00:11:34.18	00:11:35.09	00:11:35.16	25	16	7
1	29	00:11:53.14	n	smartie	h			Yes	Yes										00:11:54.07	00:11:56.04	00:11:56.10	18	47	6
1	30	00:12:11.22	n	smartie	h			Yes	Yes	Yes									00:12:12.12	00:12:13.08	00:12:14.06	15	21	23
1	31	00:12:37.19	n	black grape	h			Yes	Yes										00:12:38.12	00:12:40.01	00:12:40.08	18	39	7
1	32	00:13:00.11	n	almond	h			Yes	Yes	Yes									00:13:01.07	00:13:02.04	00:13:03.03	21	22	24
1	33	00:13:24.10	n	banana	h			Yes	Yes	Yes									00:13:25.03	00:13:25.24	00:13:26.22	18	21	23
1	34	00:13:48.20	c	cabbage	l	malteser	h	No	Yes										00:13:49.20	00:13:51.13	00:13:51.24	25	43	11
1	35	00:14:19.02	n	black grape	h			Yes	Yes	Yes									00:14:19.18	00:14:20.12	00:14:20.18	16	19	6
1	36	00:14:41.23	n	black grape	h			No	Yes	Yes									00:14:42.18	00:14:43.12	00:14:43.20	20	19	8
1	37	00:15:00.15	n	banana	h			Yes	Yes										00:15:01.11	00:15:02.18	00:15:03.06	21	32	13
1	38	00:15:23.12	n	smartie	h			Yes	Yes										00:15:24.05	00:15:26.08	00:15:26.16	18	53	8
1	39	00:15:45.16	n	black grape	h			Yes	Yes	Yes									00:15:46.07	00:15:46.24	00:15:47.10	16	17	11
1	40	00:16:05.19	n	smartie	h			Yes	Yes										00:16:06.13	00:16:09.07	00:16:09.15	19	69	8
1	41	00:16:26.24	n	black grape	h			Yes	Yes										00:16:27.18	00:16:29.16	00:16:30.00	19	48	9
1	42	00:16:50.02	n	malteser	h			Yes	Yes	Yes									00:16:50.20	00:16:51.16	00:16:53.00	18	21	34
1	43	00:17:08.15	n	smartie	h			Yes	Yes	Yes									00:17:09.09	00:17:10.05	00:17:10.20	19	21	15
1	44	00:17:33.17	c	malteser	h	cabbage	l	Yes	Yes										00:17:34.14	00:17:37.12		22	73	

1	45	00:18:07.23	n	black grape	h			No	Yes						Yes					00:18:08.17	00:18:10.06	00:18:10.16	19	39	10
1	46	00:18:32.12	n	black grape	h			No	Yes	Yes						Yes			Yes	00:18:33.13	00:18:34.08	00:18:36.00	26	20	42
1	47	00:18:56.03	n	malteser	h			Yes	Yes					Yes		Yes				00:18:56.22			19		
1	48	00:19:31.08	n	banana	h			No	Yes	Yes										00:19:32.10	00:19:33.04	00:19:34.11	27	19	32
1	49	00:19:52.11	n	black grape	h			No	Yes											00:19:53.04	00:19:53.23	00:19:56.21	18	19	73
1	50	00:20:11.19	n	smartie	h			No	Yes	Yes										00:20:12.18	00:20:13.11	00:20:14.02	24	18	16
1	51	00:20:37.22	n	black grape	h			Yes	Yes	Yes										00:20:38.15	00:20:39.08	00:20:40.14	18	18	31
1	52	00:20:54.22	n	black grape	h			Yes	Yes	Yes										00:20:55.15	00:20:56.07	00:20:56.14	18	17	7
1	53	00:21:14.08	n	smartie	h			Yes	Yes											00:21:15.00	00:21:16.05	00:21:21.17	17	30	137
1	54	00:21:37.08	n	malteser	h			Yes	Yes											00:21:37.23	00:21:39.00	00:21:40.14	15	27	39
1	55	00:22:04.07	n	black grape	h			Yes	Yes	Yes										00:22:04.24	00:22:05.16	00:22:05.21	17	17	5
1	56	00:22:33.04	c	black grape	h	nothing	l	Yes	Yes											00:22:33.22	00:22:37.07		18	85	
1	57	00:23:02.08	n	black grape	h			Yes	Yes											00:23:03.02	00:23:05.17	00:23:05.22	19	65	5
1	58	00:23:19.04	n	malteser	h			Yes	Yes	Yes								Yes		00:23:19.22	00:23:21.01	00:23:21.10	18	29	9
1	59	00:23:40.16	n	black grape	h			Yes	Yes	Yes										00:23:41.11	00:23:42.04	00:23:42.12	20	18	8
1	60	00:24:03.16	n	malteser	h			Yes	Yes	Yes										00:24:04.09	00:24:05.07	00:24:07.00	18	23	43
1	61	00:24:26.04	n	black grape	h			No	Yes										Yes	00:24:26.23	00:24:28.13	00:24:28.21	19	40	8
1	62	00:24:58.22	n	black grape	h			Yes	Yes	Yes				Yes						00:24:59.16	00:25:00.08	00:25:02.11	19	17	53
1	63	00:25:22.08	n	cabbage	l			No	No								Yes								
1	64	00:26:08.06	n	smartie	h			Yes	Yes						Yes	Yes	Yes			00:26:09.08	00:26:10.24	00:26:11.04	27	41	5
1	65	00:26:43.19	c	black grape	h	smartie	h	Yes	Yes	Yes					Yes				Yes	00:26:44.10	00:26:45.04	00:26:46.12	16	19	33
1	66	00:27:07.16	n	black grape	h			Yes	Yes	Yes				Yes						00:27:08.09	00:27:09.02	00:27:10.08	18	18	31
1	67	00:27:27.11	n	malteser	h			Yes	Yes	Yes										00:27:28.02	00:27:28.24	00:27:30.09	16	22	35
1	68	00:27:47.03	n	smartie	h			Yes	Yes											00:27:47.23	00:27:49.08	00:27:49.14	20	35	6
1	69	00:28:13.19	n	black grape	h			Yes	Yes	Yes										00:28:14.12	00:28:15.05	00:28:15.19	18	18	14
1	70	00:28:29.16	n	smartie	h			Yes	Yes											00:28:30.12	00:28:35.00	00:28:35.06	21	113	6
1	71	00:28:49.01	n	black grape	h			No	Yes			Yes				Yes				00:28:50.01	00:28:52.01	00:28:52.08	25	50	7
2	1	00:29:40.11	n	apple	l			No	Yes	Yes										00:29:41.13	00:29:42.10	00:29:42.20	27	22	10
2	2	00:29:57.08	n	carrot	l			No	Yes	Yes										00:29:58.06	00:29:59.05	00:29:59.15	23	24	10
2	3	00:30:12.18	n	cabbage	l			Yes	Yes	Yes										00:30:13.13	00:30:14.09	00:30:14.17	20	21	8
2	4	00:30:35.21	c	cabbage	l	carrot	l	No	Yes				Yes							00:30:36.20	00:30:39.03	00:30:39.10	24	58	7
2	5	00:31:27.03	n	pear	h			Yes	Yes											00:31:27.24	00:31:32.24	00:31:33.04	21	125	5
2	6	00:32:01.08	n	apple	l			No	Yes	Yes										00:32:02.04	00:32:02.24	00:32:04.04	21	20	30
2	7	00:32:22.06	n	apple	l			Yes	Yes											00:32:23.03	00:32:24.11	00:32:24.21	22	33	10
2	8	00:32:51.01	c	carrot	l	malteser	h	No	Yes											00:32:51.22	00:32:54.13	00:32:54.20	21	66	7
2	9	00:33:21.24	n	black grape	h			Yes	Yes											00:33:22.18	00:33:24.19	00:33:25.00	19	51	6
2	10	00:33:52.16	n	black grape	h			Yes	Yes											00:33:53.10	00:33:54.22	00:33:55.02	19	37	5
2	11	00:34:07.17	n	apple	l			No	Yes			Yes								00:34:08.15	00:34:10.06		23	41	
2	12	00:34:26.19	n	pear	h			No	Yes	Yes										00:34:27.14	00:34:28.11	00:34:28.21	20	22	10
2	13	00:34:44.15	n	smartie	h			Yes	Yes	Yes										00:34:45.10	00:34:46.05	00:34:46.15	20	20	10
2	14	00:34:59.09	n	malteser	h			Yes	Yes	Yes										00:35:00.02	00:35:01.05	00:35:02.13	18	28	33
2	15	00:35:18.11	n	smartie	h			Yes	Yes			Yes								00:35:19.05	00:35:20.22	00:35:22.16	19	42	44
2	16	00:35:36.05	n	black grape	h			Yes	Yes	Yes										00:35:36.24	00:35:37.17	00:35:38.06	19	18	14
2	17	00:35:52.21	n	black grape	h			Yes	Yes											00:35:53.16	00:35:58.07	00:35:58.13	20	116	6
2	18	00:36:11.06	n	banana	h			No	Yes	Yes										00:36:12.02	00:36:12.18	00:36:12.24	21	16	6
2	19	00:36:26.22	n	smartie	h			Yes	Yes											00:36:27.15	00:36:29.18	00:36:30.01	18	53	8
2	20	00:36:46.13	c	black grape	h	nothing	l	Yes	Yes											00:36:47.06	00:36:50.10		18	79	
2	21	00:37:12.21	n	strawberry	h			Yes	Yes											00:37:13.12	00:37:14.09	00:37:14.22	16	22	13
2	22	00:37:30.05	n	malteser	h			Yes	Yes	Yes										00:37:30.23	00:37:31.15	00:37:32.01	18	17	11

2	23	00:37:46.18	n	smartie	h			Yes	Yes	Yes											00:37:47.12	00:37:48.07	00:37:48.22	19	20	15
2	24	00:38:00.17	n	black grape	h			Yes	Yes												00:38:01.11	00:38:02.14	00:38:02.24	19	28	10
2	25	00:38:19.23	n	banana	h			Yes	Yes	Yes											00:38:20.14	00:38:21.07	00:38:21.13	16	18	6
2	26	00:38:41.12	c	malteser	h	carrot	l	Yes	Yes			Yes									00:38:42.07	00:38:49.00		20	168	
2	27	00:39:13.18	n	strawberry	h			Yes	Yes												00:39:14.11	00:39:16.21	00:39:17.09	18	60	13
2	28	00:39:36.11	n	smartie	h			No	No																	
2	29	00:40:17.18	n	black grape	h			No	No																	
2	30	00:40:48.16	n	malteser	h			Yes	Yes	Yes											00:40:49.10	00:40:50.14	00:40:50.21	19	29	7
2	31	00:41:07.15	n	black grape	h			No	No																	
2	32	00:41:46.11	n	banana	h			No	No																	
2	33	00:42:32.21	n	strawberry	h			Yes	Yes												00:42:33.20	00:42:36.23	00:42:37.06	24	78	8
2	34	00:42:51.00	n	banana	h			No	No																	
2	35	00:43:39.23	n	malteser	h			Yes	Yes	Yes											00:43:40.20	00:43:41.19	00:43:42.16	22	24	22
2	36	00:43:57.04	n	malteser	h			Yes	Yes	Yes											00:43:57.23	00:43:58.24	00:43:59.05	19	26	6
2	37	00:44:13.19	n	nothing	l			No	No																	
2	38	00:44:39.06	n	strawberry	h			Yes	Yes	Yes											00:44:40.00	00:44:41.10	00:44:41.16	19	35	6
2	39	00:45:03.16	n	smartie	h			No	Yes	Yes											00:45:04.17	00:45:05.24	00:45:08.10	26	32	61
2	40	00:45:22.22	n	black grape	h			Yes	Yes												00:45:23.17	00:45:25.16	00:45:26.13	20	49	22
2	41	00:45:51.09	c	banana	h	strawberry	h	Yes	Yes												00:45:52.24	00:45:55.04	00:45:55.11	40	55	7
2	42	00:46:23.04	n	malteser	h			Yes	Yes												00:46:24.01	00:46:25.22	00:46:26.22	22	46	25
2	43	00:46:46.02	n	black grape	h			Yes	Yes	Yes											00:46:46.24	00:46:48.02	00:46:48.10	22	28	8
2	44	00:47:01.23	n	banana	h			Yes	Yes	Yes											00:47:02.18	00:47:03.18	00:47:04.03	20	25	10
2	45	00:47:19.00	n	smartie	h			No	No																	
2	46	00:47:52.11	n	malteser	h			Yes	Yes												00:47:53.07	00:47:55.00	00:47:56.01	21	43	26
2	47	00:48:10.16	n	black grape	h			Yes	Yes	Yes			Yes								00:48:11.15	00:48:12.14	00:48:12.21	24	24	7
2	48	00:48:30.07	n	malteser	h			Yes	Yes												00:48:30.23	00:48:33.08	00:48:33.14	16	60	6
2	49	00:48:49.00	n	banana	h			No	Yes												00:48:50.01	00:48:51.16	00:48:51.23	26	40	7
2	50	00:49:08.12	n	malteser	h			Yes	Yes	Yes											00:49:09.06	00:49:12.19	00:49:13.06	19	88	12
2	51	00:49:36.15	c	strawberry	h	banana	h	Yes	Yes	Yes											00:49:37.17	00:49:38.17	00:49:39.10	27	25	18
2	52	00:50:11.03	n	smartie	h			No	No											Yes						
2	53	00:50:42.10	n	malteser	h			No	No																	
2	54	00:51:22.08	n	pear	h			No	No											Yes						
2	55	00:52:09.24	n	black grape	h			No	No								Yes			Yes						
2	56	00:52:36.19	n	black grape	h			No	Yes	Yes							Yes				00:52:38.04	00:52:38.23	00:52:39.04	35	19	6
2	57	00:52:53.10	n	black grape	h			No	No																	
2	58	00:52:16.06	n	black grape	h			No	No											Yes						
2	59	00:53:42.21	n	malteser	h			Yes	Yes												00:53:43.23	00:53:45.18	00:53:46.06	27	45	13
2	60	00:54:01.01	n	malteser	h			Yes	Yes	Yes											00:54:01.21	00:54:02.18	00:54:03.00	20	22	7
2	61	00:54:17.12	n	strawberry	h			Yes	Yes	Yes			Yes								00:54:18.05	00:54:20.03	00:54:20.18	18	48	15
2	62	00:54:50.15	n	black grape	h			No	Yes												00:54:51.16	00:54:55.05	00:54:55.10	26	89	5
2	63	00:55:09.17	n	almond	h			No	Yes				Yes								00:55:10.13	00:55:11.20	00:55:12.21	21	32	26
2	64	00:55:44.02	n	caschew nut	h			No	Yes												00:55:45.02	00:55:47.21	00:55:48.05	25	69	9
2	65	00:56:06.12	n	black grape	h			Yes	Yes	Yes											00:56:07.04	00:56:08.02	00:56:08.15	17	23	13
2	66	00:56:28.11	n	almond	h			Yes	Yes	Yes											00:56:29.04	00:56:29.24	00:56:30.13	18	20	14
2	67	00:56:51.08	n	black grape	h			Yes	Yes												00:56:52.01	00:56:54.03	00:56:54.09	18	52	6
2	68	00:57:09.24	n	m and m	h			Yes	Yes	Yes											00:57:10.14	00:57:11.07	00:57:13.06	15	18	49
2	69	00:57:37.07	n	black grape	h			No	Yes												00:57:39.23	00:57:41.24	00:57:49.02	66	51	178
2	70	00:58:16.17	n	pear	h			Yes	Yes												00:58:17.12	00:58:20.03	00:58:20.13	20	66	10
2	71	00:58:34.18	n	smartie	h			Yes	Yes												00:58:35.10	00:58:36.11	00:58:37.01	17	26	15

2	72	00:58:55.24	c	almond	h	black grape	h	Yes	Yes												00:58:56.21	00:58:59.09	00:59:00.16	22	63	32
2	73	00:59:23.07	n	almond	h			No	Yes												00:59:24.03	00:59:25.13	00:59:26.20	21	60	7
2	74	00:59:46.09	n	black grape	h			Yes	Yes	Yes											00:59:47.02	00:59:49.01	00:59:49.08	18	49	7
2	75	01:00:11.11	n	cabbage	l			Yes	Yes	Yes											01:00:12.06	01:00:13.02	01:00:13.09	20	21	7
2	76	01:00:31.23	n	black grape	h			Yes	Yes	Yes					Yes	Yes					01:00:32.21	01:00:33.17	01:00:34.03	23	21	11
2	77	01:00:50.13	n	almond	h			No	Yes				Yes								01:00:51.08	01:00:52.23	01:00:53.06	20	40	8
2	78	01:01:14.18	n	carrot	l			No	Yes	Yes											01:01:15.14	01:01:16.16	01:01:20.16	21	27	100
2	79	01:01:38.01	n	black grape	h			No	Yes	Yes											01:01:38.23	01:01:39.18	01:01:40.01	22	20	8
2	80	01:01:58.05	n	black grape	h			No	Yes	Yes											01:01:59.04	01:01:59.24	01:02:00.11	24	20	12
2	81	01:02:16.06	n	almond	h			No	Yes												01:02:17.07	01:02:19.03	01:02:20.21	27	46	43
2	82	01:02:41.10	n	nothing	l			No	Yes												01:02:42.10	01:02:43.14		25	29	
2	83	01:03:07.10	n	pear	h			No	Yes												01:03:08.05	01:03:10.04	01:03:11.19	20	49	40
2	84	01:03:31.28	n	black grape	h			No	No																	
2	85	01:03:51.11	n	black grape	h			No	No																	
2	86	01:04:29.18	n	carrot	l			No	No																	
2	87	01:05:08.18	n	almond	h			No	Yes	Yes					Yes	Yes					01:05:09.19	01:05:10.11	01:05:10.18	26	17	7
2	88	01:05:39.18	c	almond	h	cabbage	l	Yes	Yes	Yes					Yes				Yes		01:05:40.07	01:05:41.12	01:05:41.19	14	80	7
2	89	01:06:13.13	n	almond	h			Yes	Yes	Yes				Yes	Yes	Yes					01:06:14.10	01:06:15.05	01:06:16.03	22	20	23
2	90	01:06:35.19	n	cabbage	l			No	Yes									Yes			01:06:40.13	01:06:41.20		119	32	
2	91	01:07:16.17	n	almond	h			No	No									Yes								
2	92	01:07:35.13	n	almond	h			No	Yes	Yes						Yes					01:07:37.04	01:07:38.04	01:07:39.07	41	25	28
2	93	01:07:56.08	n	black grape	h			Yes	Yes	Yes											01:07:57.02	01:07:58.09	01:07:58.18	19	32	9
2	94	01:08:14.04	n	almond	h			Yes	Yes												01:08:14.21	01:08:17.15	01:08:17.20	17	69	5
2	95	01:08:39.09	n	black grape	h			Yes	Yes												01:08:40.02	01:08:42.05	01:08:42.11	18	53	6
2	96	01:08:58.19	n	almond	h			Yes	Yes	Yes											01:08:59.14	01:09:00.09	01:09:00.15	20	20	6
2	97	01:09:17.06	n	black grape	h			Yes	Yes												01:09:18.00	01:09:20.12	01:09:20.17	19	62	5
2	98	01:09:37.17	n	smartie	h			No	Yes												01:09:38.14	01:09:40.24	01:09:41.05	22	60	6
2	99	01:10:03.19	n	black grape	h			No	No									Yes	Yes							
2	100	01:10:51.14	n	smartie	h			Yes	Yes					Yes							01:10:52.10	01:10:54.07	01:10:54.15	21	47	8
2	101	01:11:11.09	n	smartie	h			No	Yes	Yes											01:11:12.05	01:11:13.05	01:11:13.13	21	25	8
3	1	01:12:53.06	n	carrot	l			Yes	Yes	Yes											01:12:54.02	01:12:55.04	01:12:55.10	21	27	6
3	2	01:13:16.24	n	cabbage	l			No	Yes												01:13:18.00	01:13:19.00		26	25	
3	3	01:13:37.02	n	apple	l			Yes	Yes	Yes											01:13:38.05	01:13:39.00	01:13:39.06	28	20	6
3	4	01:14:01.20	n	apple	l			Yes	Yes	Yes											01:14:03.10	01:14:04.17	01:14:04.24	40	32	7
3	5	01:14:23.08	n	carrot	l			No	No																	
3	6	01:14:48.15	n	apple	l			Yes	Yes												01:14:49.15	01:14:51.01	01:14:51.07	25	36	6
3	7	01:15:07.04	n	pear	h			Yes	Yes	Yes											01:15:08.01	01:15:08.23	01:15:09.20	22	22	22
3	8	01:15:28.24	c	carrot	l	cabbage	l	No	Yes	Yes											01:15:30.12	01:15:32.17	01:15:32.21	38	55	4
3	9	01:16:05.14	n	apple	l			Yes	No																	
3	10	01:16:29.23	n	pear	h			Yes	No										Yes							
3	11	01:16:55.11	n	plum	h			Yes	Yes					Yes							01:16:57.15	01:17:00.01	01:17:00.05	54	61	4
3	12	01:17:22.18	c	apricot	h	nothing	l	Yes	Yes												01:17:25.03	01:17:27.00		60	47	
3	13	01:17:52.07	n	smartie	h			Yes	No									Yes	Yes							
3	14	01:18:31.18	n	apple	l			No	No					Yes				Yes	Yes							
3	15	01:19:13.00	n	black grape	h			Yes	Yes	Yes				Yes	Yes						01:19:13.20	01:19:14.16	01:19:15.01	20	21	10
3	16	01:19:29.03	n	apricot	h			No	Yes												01:19:36.19	01:19:38.12	01:19:39.01	191	43	14
3	17	01:20:02.10	n	plum	h			Yes	No									Yes								
3	18	01:20:27.01	n	banana	h			Yes	Yes	Yes					Yes						01:20:27.21	01:20:28.12	01:20:28.17	20	16	5
3	19	01:20:41.09	n	black grape	h			Yes	Yes												01:20:42.04	01:20:43.16	01:20:43.22	20	37	6

3	20	01:20:58.12	n	smartie	h			Yes	Yes	Yes										01:20:59.06	01:21:00.07	01:21:00.22	19	26	15
3	21	01:21:16.05	n	strawberry	h			Yes	Yes											01:21:16.21	01:21:18.15	01:21:19.08	16	44	18
3	22	01:21:38.20	n	malteser	h			Yes	Yes	Yes										01:21:39.15	01:21:40.07	01:21:41.08	20	17	26
3	23	01:21:57.18	n	nothing	l			Yes	Yes											01:21:58.14	01:21:59.10		21	21	
3	24	01:22:18.22	n	strawberry	h			Yes	Yes	Yes										01:22:19.17	01:22:20.11	01:22:20.17	20	19	6
3	25	01:22:36.23	n	smartie	h			Yes	Yes											01:22:37.16	01:22:39.21	01:22:40.02	18	55	6
3	26	01:23:00.02	n	white grape	h			Yes	Yes	Yes										01:23:00.20	01:23:02.00	01:23:02.06	18	30	6
3	27	01:23:28.11	c	banana	h	malteser	h	Yes	Yes	Yes										01:23:29.06	01:23:30.11	01:23:31.15	20	30	29
3	28	01:24:03.10	n	plum	h			Yes	Yes											01:24:04.09	01:24:06.08	01:24:06.13	24	49	5
3	29	01:24:37.20	n	banana	h			Yes	Yes											01:24:38.13	01:24:39.20	01:24:40.00	18	32	5
3	30	01:24:57.03	n	white grape	h			Yes	Yes											01:24:57.22	01:25:00.13	01:25:00.21	19	66	8
3	31	01:25:14.15	n	black grape	h			Yes	Yes	Yes										01:25:15.07	01:25:16.06	01:25:16.13	17	24	7
3	32	01:25:33.11	n	cabbage	l			Yes	Yes	Yes		Yes							Yes	01:25:34.06	01:25:35.07		20	26	
3	33	01:26:02.21	n	malteser	h			Yes	Yes	Yes				Yes							01:26:04.23	01:26:06.04			31
3	34	01:26:32.04	n	smartie	h			No	Yes												01:26:33.21	01:26:35.00			29
3	35	01:26:53.19	n	apricot	h			No	Yes											01:26:54.11	01:26:55.24	01:26:56.06	17	38	7
3	36	01:27:11.01	n	black grape	h			Yes	Yes	Yes										01:27:11.19	01:27:12.11	01:27:15.14	18	17	78
3	37	01:27:36.07	n	nothing	l			Yes	Yes						Yes				Yes		01:27:38.04				
3	38	01:28:00.10	n	banana	h			No	Yes	Yes				Yes	Yes					01:28:01.12	01:28:02.04	01:28:02.24	27	17	20
3	39	01:28:18.06	n	black grape	h			No	Yes											01:28:19.03	01:28:22.05	01:28:22.12	22	77	7
3	40	01:28:37.09	c	carrot	l	nothing	l	No	Yes											01:28:38.10	01:28:39.12		26	27	
3	41	01:29:08.04	n	malteser	h			Yes	Yes	Yes										01:29:08.24	01:29:09.16	01:29:11.22	20	17	56
3	42	01:29:46.05	n	strawberry	h			Yes	Yes	Yes						Yes				01:29:46.22	01:29:47.14	01:29:48.16	17	17	27
3	43	01:30:11.03	n	almond	h			Yes	Yes			Yes								01:30:11.23	01:30:12.22	01:30:14.06	20	24	34
3	44	01:30:42.14	n	apple	l			Yes	Yes	Yes										01:30:43.09	01:30:44.04	01:30:45.04	20	20	25
3	45	01:30:59.20	n	black grape	h			Yes	Yes	Yes										01:31:00.14	01:31:01.15	01:31:01.22	19	26	7
3	46	01:31:24.05	n	plum	h			Yes	Yes											01:31:24.23	01:31:26.05	01:31:26.09	18	32	4
3	47	01:32:01.23	c	strawberry	h	banana	h	Yes	Yes	Yes									Yes	01:32:02.18	01:32:03.16	01:32:04.04	20	23	13
3	48	01:32:30.20	n	apricot	h			Yes	Yes	Yes				Yes	Yes					01:32:31.12	01:32:32.11	01:32:33.05	17	24	19
3	49	01:32:47.14	n	black grape	h			No	Yes											01:32:48.07	01:32:50.02	01:32:50.24	18	45	22
3	50	01:33:08.01	n	malteser	h			Yes	Yes	Yes										01:33:08.19	01:33:09.14	01:33:10.12	18	20	23
3	51	01:33:23.19	n	nothing	l			No	No																
3	52	01:33:55.20	n	black grape	h			No	Yes	Yes										01:33:57.22	01:33:58.17	01:33:59.00	52	20	8
3	53	01:34:17.17	n	strawberry	h			Yes	Yes	Yes										01:34:18.10	01:34:19.04	01:34:20.02	18	19	23
3	54	01:34:35.10	n	white grape	h			No	Yes	Yes										01:34:36.06	01:34:37.01	01:34:38.05	21	20	29
3	55	01:34:51.16	n	smartie	h			Yes	Yes											01:34:52.10	01:34:53.23	01:34:54.24	19	38	26
3	56	01:35:12.16	n	banana	h			Yes	Yes	Yes										01:35:13.08	01:35:13.24	01:35:14.19	17	16	20
3	57	01:35:36.21	n	white grape	h			No	Yes	Yes										01:35:37.24	01:35:38.19	01:35:39.02	28	20	8
3	58	01:36:04.19	c	strawberry	h	nothing	l	Yes	Yes						Yes	Yes			Yes	01:36:05.12	01:36:07.16		18	54	
3	59	01:36:33.01	n	black grape	h			No	Yes				Yes							01:36:33.22	01:36:35.14	01:36:35.18	21	42	4
3	60	01:36:51.09	n	banana	h			Yes	Yes	Yes		Yes								01:36:52.06	01:36:53.01	01:36:53.24	22	20	23
3	61	01:37:21.24	n	strawberry	h			Yes	Yes											01:37:22.16	01:37:24.02	01:37:24.06	17	36	4
3	62	01:37:50.22	n	black grape	h			No	Yes	Yes										01:37:51.18	01:37:52.16	01:37:55.21	21	23	80
3	63	01:38:09.06	n	smartie	h			Yes	Yes											01:38:09.24	01:38:11.16	01:38:11.20	18	42	4
3	64	01:38:28.03	n	white grape	h			Yes	Yes	Yes										01:38:28.22	01:38:29.18	01:38:30.12	19	21	19
3	65	01:38:45.08	n	strawberry	h			Yes	Yes											01:38:45.23	01:38:47.11	01:38:47.19	15	38	8
3	66	01:39:06.21	n	apricot	h			No	Yes								Yes			01:39:08.02			31		
3	67	01:39:36.23	n	black grape	h			No	No						Yes	Yes	Yes	Yes							
3	68	01:40:22.22	n	malteser	h			Yes	Yes	Yes				Yes	Yes					01:40:23.13	01:40:24.09	01:40:25.04	16	21	20

3	69	01:40:41.14	n	black grape	h			No	No						Yes	Yes		Yes							
3	70	01:41:05.03	n	white grape	h			No	No					Yes	Yes	Yes		Yes							
3	71	01:41:36.12	n	strawberry	h			No	Yes					Yes	Yes	Yes			01:41:38.18	01:41:40.21	01:41:41.01	56	53	5
3	72	01:41:55.10	n	malteser	h			No	Yes	Yes									01:41:56.04	01:41:56.21	01:41:57.19	19	17	23
3	73	01:42:19.00	n	strawberry	h			Yes	Yes	Yes									01:42:19.20	01:42:20.17	01:42:21.18	20	22	26
3	74	01:42:46.02	c	malteser	h	carrot	l	No	Yes	Yes									01:42:46.22	01:42:47.16	01:42:51.16	20	19	100
3	75	01:43:18.01	n	apricot	h			No	Yes	Yes									01:43:18.21	01:43:19.10	01:43:19.18	20	14	8
3	76	01:43:37.08	n	black grape	h			Yes	Yes	Yes									01:43:38.02	01:43:38.23	01:43:39.04	19	21	6
3	77	01:43:54.09	n	white grape	h			No	Yes	Yes			Yes						01:43:55.08	01:43:56.04	01:43:58.18	24	21	64
3	78	01:44:13.08	n	banana	h			Yes	Yes						Yes				01:44:14.08	01:44:15.06	01:44:15.11	25	23	5
3	79	01:44:33.00	n	carrot	l			No	Yes	Yes		Yes				Yes		Yes	01:44:33.22	01:44:34.14	01:44:34.22	22	17	8
3	80	01:44:55.15	n	malteser	h			Yes	Yes	Yes				Yes					01:44:56.05	01:44:56.24	01:44:58.00	15	19	26
3	81	01:45:13.00	n	malteser	h			Yes	Yes	Yes									01:45:13.13	01:45:14.11	01:45:15.10	13	23	24
3	82	01:45:42.24	c	black grape	h	strawberry	h	No	Yes							Yes			Jammed	01:45:47.23	01:45:48.16			18
3	83	01:46:26.24	n	apricot	h			No	No								Yes	Yes						
3	84	01:46:54.20	n	malteser	h			Yes	Yes	Yes				Yes		Yes		Yes	01:46:55.14	01:46:56.09	01:46:57.08	19	20	24
3	85	01:47:16.04	n	banana	h			No	Yes	Yes				Yes	Yes				01:47:17.08	01:47:18.18	01:47:18.22	29	35	4
3	86	01:47:37.15	n	black grape	h			Yes	Yes	Yes									01:47:38.19	01:47:39.15	01:47:40.15	29	21	25
3	87	01:47:54.13	n	nothing	l			No	No															
3	88	01:48:15.01	n	cabbage	l			No	No															
3	89	01:48:42.10	n	strawberry	h			No	No															
3	90	01:49:12.11	n	plum	h			No	No															
3	91	01:49:43.03	n	black grape	h			No	No															
3	92	01:50:05.13	n	smartie	h			No	No															
4	1	00:00:24.12	n	carrot	l			No	No															
4	2	00:00:59.05	n	apple	l			Yes	Yes	Yes									00:01:00.03	00:01:01.05	00:01:02.05	23	27	25
4	3	00:01:14.22	n	apple	l			Yes	Yes	Yes									00:01:15.17	00:01:16.13	00:01:17.21	20	21	33
4	4	00:01:34.03	n	cabbage	l			No	Yes	Yes			Yes				Yes		00:01:34.24	00:01:35.21	00:01:36.04	21	22	8
4	5	00:02:18.00	n	carrot	l			No	Yes	Yes									00:02:19.01	00:02:19.21	00:02:20.03	26	20	7
4	6	00:02:42.08	n	cabbage	l			No	No															
4	7	00:03:26.11	c	apple	l	carrot	l	No	Yes										00:03:27.03	00:03:30.16	00:03:31.09	17	88	18
4	8	00:03:56.05	n	pear	h			Yes	Yes										00:03:56.21	00:03:57.16	00:03:57.22	16	20	6
4	9	00:04:14.22	n	white grape	h			Yes	Yes	Yes									00:04:15.13	00:04:16.06	00:04:17.09	16	20	26
4	10	00:04:31.18	n	smartie	h			Yes	Yes	Yes									00:04:32.09	00:04:33.05	00:04:34.02	16	21	22
4	11	00:04:53.20	n	plum	h			Yes	Yes	Yes			Yes						00:04:54.11	00:04:55.05	00:04:55.10	16	19	5
4	12	00:05:21.08	n	malteser	h			Yes	Yes	Yes									00:05:22.15	00:05:23.10	00:05:24.09	32	20	24
4	13	00:05:46.18	n	strawberry	h			Yes	Yes	Yes									00:05:47.09	00:05:48.03	00:05:48.08	16	19	5
4	14	00:06:20.17	n	peach	h			Yes	Yes										00:06:21.07	00:06:23.05	00:06:23.10	15	48	5
4	15	00:06:52.11	c	carrot	l	malteser	h	No	Yes										00:06:53.02	00:06:55.03	00:06:56.07	16	51	29
4	16	00:08:00.11	n	pear	h			Yes	Yes	Yes									00:08:01.00	00:08:01.19	00:08:02.01	14	19	7
4	17	00:08:19.11	n	white grape	h			Yes	Yes	Yes									00:08:19.24	00:08:20.15	00:08:20.19	13	16	4
4	18	00:08:36.05	n	black grape	h			Yes	Yes										00:08:36.20	00:08:39.02	00:08:39.09	15	57	7
4	19	00:08:55.12	n	nothing	l			No	Yes						Yes			Yes	00:08:56.01	00:08:56.24		14	23	
4	20	00:09:12.22	n	white grape	h			Yes	Yes	Yes			Yes	Yes					00:09:13.14	00:09:14.07	00:09:14.15	17	18	8
4	21	00:09:33.13	n	carrot	l			Yes	Yes	Yes									00:09:34.03	00:09:34.22	00:09:35.09	15	19	12
4	22	00:09:55.14	n	malteser	h			Yes	Yes	Yes									00:09:56.04	00:09:57.04	00:09:57.08	15	25	4
4	23	00:10:16.03	n	peach	h			Yes	Yes	Yes									00:10:16.16	00:10:17.08	00:10:17.13	13	17	5
4	24	00:10:34.20	n	white grape	h			No	Yes	Yes									00:10:35.10	00:10:36.03	00:10:36.11	15	18	8
4	25	00:10:53.02	c	carrot	l	nothing	l	Yes	Yes										00:10:53.18	00:10:54.14		16	21	

4	26	00:11:21.20	n	black grape	h			Yes	Yes											00:11:22.09	00:11:23.23	00:11:25.24	14	39	51
4	27	00:11:46.04	n	plum	h			No	Yes	Yes										00:11:46.21	00:11:47.17	00:11:48.19	17	21	27
4	28	00:12:06.12	n	malteser	h			Yes	Yes	Yes										00:12:07.01	00:12:07.19	00:12:08.15	14	18	21
4	29	00:12:30.13	n	apple	l			No	Yes	Yes										00:12:31.05	00:12:31.24	00:12:32.07	17	19	8
4	30	00:12:49.06	n	white grape	h			No	Yes			Yes									00:12:52.10				
4	31	00:13:16.13	n	smartie	h			No	Yes										Yes	00:13:17.03	00:13:18.12	00:13:19.19	15	34	32
4	32	00:13:40.23	n	black grape	h			Yes	Yes	Yes										00:13:41.16	00:13:42.10	00:13:42.15	18	19	5
4	33	00:14:15.19	n	apple	l			No	Yes				Yes							00:14:16.11	00:14:17.18	00:14:18.03	17	32	10
4	34	00:14:37.04	n	malteser	h			Yes	Yes	Yes										00:14:37.18	00:14:38.12	00:14:39.10	14	19	23
4	35	00:14:59.18	n	cabbage	l			No	Yes	Yes		Yes								00:15:01.20	00:15:02.20		52	25	
4	36	00:15:20.24	n	peach	h			Yes	Yes											00:15:21.14	00:15:23.03	00:15:23.09	15	39	6
4	37	00:15:49.05	c	malteser	h	cabbage	l	Yes	Yes										Yes	00:15:49.22	00:15:51.24		17	52	
4	38	00:16:18.01	n	black grape	h			Yes	Yes	Yes				Yes						00:16:18.15	00:16:19.20	00:16:20.21	14	30	26
4	39	00:16:38.08	n	white grape	h			No	Yes	Yes										00:16:39.01	00:16:39.19	00:16:39.24	18	18	5
4	40	00:17:03.04	n	malteser	h			Yes	Yes	Yes										00:17:03.19	00:17:04.14	00:17:07.15	15	20	76
4	41	00:17:27.03	n	pear	h			Yes	Yes	Yes										00:17:27.18	00:17:28.08	00:17:28.14	15	15	6
4	42	00:17:46.12	n	plum	h			No	Yes											00:17:47.08	00:17:49.09	00:17:49.19	21	51	10
4	43	00:18:09.24	n	white grape	h			No	No																
4	44	00:18:32.21	n	malteser	h			No	Yes	Yes										00:18:33.14	00:18:34.10	00:18:34.15	18	21	5
4	45	00:18:55.09	n	apple	l			No	No																
4	46	00:19:20.08	n	black grape	h			No	No																
4	47	00:19:52.03	n	peach	h			Yes	Yes	Yes										00:19:52.18	00:19:53.10	00:19:53.15	15	17	5
4	48	00:20:10.15	n	black grape	h			No	Yes	Yes			Yes							00:20:11.11	00:20:12.04	00:20:12.12	21	18	8
4	49	00:20:38.11	c	apple	l	nothing	l	Yes	Yes							Yes			Yes	00:20:39.03	00:20:40.02		17	24	
4	50	00:21:06.00	n	malteser	h			Yes	Yes	Yes				Yes						00:21:06.15	00:21:07.10	00:21:08.07	15	20	22
4	51	00:21:24.19	n	smartie	h			Yes	Yes	Yes										00:21:25.10	00:21:26.07	00:21:27.09	16	22	27
4	52	00:21:46.11	n	apple	l			No	Yes	Yes										00:21:47.10	00:21:48.21	00:21:49.03	24	36	7
4	53	00:22:08.17	n	white grape	h			No	Yes																
4	54	00:22:32.09	n	malteser	h			No	Yes	Yes										00:22:33.02	00:22:33.19	00:22:33.24	18	17	5
4	55	00:22:54.08	n	black grape	h			No	No																
4	56	00:23:31.05	c	peach	h	nothing	l	Yes	Yes						Yes	Yes			Yes	00:23:31.23	00:23:32.21		18	23	
4	57	00:23:58.24	n	malteser	h			No	Yes	Yes				Yes						00:23:59.17	00:24:00.10	00:24:00.17	18	18	7
4	58	00:24:18.12	n	peach	h			Yes	Yes	Yes										00:24:19.02	00:24:19.20	00:24:21.04	15	18	34
4	59	00:24:35.18	n	nothing	l			No	No						Yes										
4	60	00:24:57.20	n	malteser	h			No	Yes	Yes										00:24:58.23	00:25:00.05	00:25:00.15	28	32	10
4	61	00:25:17.10	n	pear	h			No	Yes	Yes										00:25:18.03	00:25:18.19	00:25:19.00	18	16	6
4	62	00:25:41.16	n	smartie	h			No	No																
4	63	00:26:06.12	n	peach	h			No	Yes				Yes							00:26:07.06	00:26:08.00	00:26:08.08	19	19	8
4	64	00:26:28.22	n	malteser	h			No	Yes	Yes											00:26:30.18	00:26:31.01			8
4	65	00:26:55.07	n	malteser	h			No	Yes	Yes										00:26:55.22	00:26:56.19	00:26:58.08	15	22	39
4	66	00:27:17.03	n	peach	h			Yes	Yes						Yes					00:27:17.19	00:27:18.22	00:27:20.09	16	28	37
4	67	00:27:37.13	n	smartie	h			No	No																
4	68	00:28:00.08	n	malteser	h			No	Yes	Yes										00:28:01.06	00:28:02.02	00:28:02.10	23	21	8
4	69	00:28:25.20	n	apple	l			No	No																
4	70	00:29:00.17	n	white grape	h			No	No																
4	71	00:29:26.01	n	malteser	h			No	No																
4	72	00:30:04.15	n	strawberry	h			No	Yes				Yes							00:30:05.13	00:30:07.01	00:30:07.12	23	38	11
4	73	00:30:35.24	n	malteser	h			No	Yes	Yes										00:30:36.19	00:30:37.11	00:30:37.19	20	17	8
4	74	00:30:58.09	c	malteser	h	peach	h	No	Yes											00:30:59.07	00:31:01.01	00:31:01.07	23	44	6

4	75	00:31:30.09	n	peach	h			No	Yes	Yes										00:31:31.01	00:31:32.07	00:31:32.13	17	31	6
4	76	00:31:59.07	n	black grape	h			No	Yes	Yes										00:32:00.08	00:32:00.21	00:32:01.06	21	18	7
4	77	00:32:23.00	n	malteser	h			No	Yes	Yes										00:32:23.20	00:32:24.16	00:32:24.21	20	21	5
4	78	00:32:39.19	n	apple	l			No	No																
4	79	00:33:03.00	n	malteser	h			No	Yes	Yes										00:33:05.06	00:33:05.23	00:33:07.19	56	17	46
4	80	00:33:27.24	n	black grape	h			No	Yes											00:33:28.17	00:33:32.08	00:33:32.17	18	91	9
4	81	00:33:49.02	n	smartie	h			No	Yes	Yes										00:33:49.22	00:33:50.19	00:33:51.02	20	22	8
4	82	00:34:11.12	n	black grape	h			No	Yes	Yes										00:34:12.07	00:34:13.02	00:34:13.08	20	20	6
4	83	00:34:28.19	n	malteser	h			Yes	Yes	Yes										00:34:29.08	00:34:30.02	00:34:31.01	14	19	24
4	84	00:34:45.15	n	pear	h			No	Yes											00:34:46.06	00:34:47.20	00:34:48.06	16	39	10
4	85	00:35:14.19	c	black grape	h	carrot	l	Yes	Yes										Yes	00:35:15.15	00:35:16.20		21	30	
4	86	00:35:41.18	n	malteser	h			No	Yes	Yes				Yes						00:35:42.09	00:35:43.04	00:35:43.10	16	20	6
4	87	00:36:07.14	n	pear	h			Yes	Yes	Yes						Yes				00:36:08.07	00:36:09.01	00:36:09.07	18	19	6
4	88	00:36:27.16	n	black grape	h			No	No																
4	89	00:36:48.21	n	malteser	h			No	No																
4	90	00:37:16.19	n	m and m	h			No	No																
4	91	00:37:45.11	n	black grape	h			No	No								Yes	Yes							
4	92	00:38:08.02	n	white grape	h			No	No					Yes			Yes								
5	1	00:00:21.14	n	carrot	l			Yes	Yes	Yes										00:00:22.08	00:00:23.02	00:00:23.09	19	19	7
5	2	00:00:44.15	n	apple	l			Yes	Yes	Yes										00:00:45.06	00:00:45.22	00:00:46.03	16	16	6
5	3	00:01:01.15	c	carrot	l	nothing	l	Yes	Yes										Yes	00:01:02.04	00:01:03.09		14	30	
5	4	00:01:24.11	n	apple	l			Yes	Yes	Yes				Yes						00:01:24.24	00:01:25.13	00:01:25.19	13	14	6
5	5	00:01:42.23	n	apple	l			Yes	Yes	Yes										00:01:43.13	00:01:44.03	00:01:44.09	15	15	6
5	6	00:02:00.18	n	cabbage	l			No	No																
5	7	00:02:22.02	n	apple	l			Yes	Yes	Yes										00:02:22.17	00:02:23.13	00:02:24.07	15	21	19
5	8	00:02:42.09	n	pear	h			Yes	Yes	Yes										00:02:42.22	00:02:43.14	00:02:43.20	13	17	6
5	9	00:03:03.10	c	apple	l	carrot	l	Yes	Yes	Yes										00:03:04.01	00:03:04.16	00:03:04.20	16	15	4
5	10	00:03:33.18	n	pear	h			Yes	Yes	Yes										00:03:34.10	00:03:35.00	00:03:35.04	17	15	4
5	11	00:03:50.18	n	apple	l			Yes	Yes											00:03:51.09	00:03:52.12	00:03:52.17	16	28	5
5	12	00:04:08.20	n	carrot	l			No	Yes	Yes										00:04:09.12	00:04:10.03	00:04:10.08	17	16	5
5	13	00:04:32.24	n	pear	h			Yes	Yes	Yes										00:04:33.16	00:04:34.12	00:04:34.18	17	21	6
5	14	00:04:54.20	n	malteser	h			Yes	Yes	Yes										00:04:55.10	00:04:55.24	00:04:56.04	15	14	5
5	15	00:05:17.00	n	apple	l			Yes	Yes	Yes										00:05:17.16	00:05:18.05	00:05:18.11	16	14	6
5	16	00:05:35.09	n	apple	l			Yes	Yes	Yes										00:05:36.01	00:05:36.16	00:05:36.21	17	15	5
5	17	00:06:00.02	c	carrot	l	malteser	h	No	Yes	Yes										00:06:00.22	00:06:01.13	00:06:01.21	20	16	8
5	18	00:06:27.04	n	apple	l			Yes	Yes						Yes					00:06:27.22	00:06:28.22	00:06:29.03	18	25	6
5	19	00:06:48.04	n	pear	h			Yes	Yes	Yes										00:06:48.21	00:06:49.11	00:06:49.17	17	15	6
5	20	00:07:08.11	n	carrot	l			No	Yes	Yes		Yes			Yes					00:07:09.05	00:07:09.23		19	18	
5	21	00:07:26.20	n	chocolate raisin	h			Yes	Yes	Yes										00:07:27.10	00:07:27.24	00:07:29.10	15	14	36
5	22	00:07:46.14	n	white grape	h			Yes	Yes	Yes										00:07:47.05	00:07:47.20	00:07:48.01	16	15	6
5	23	00:08:02.04	n	nothing	l			No	No						Yes		Yes								
5	24	00:08:19.00	n	apple	l			Yes	Yes	Yes										00:08:19.16	00:08:20.06	00:08:20.14	16	15	8
5	25	00:08:36.20	n	plum	h			Yes	Yes											00:08:37.11	00:08:38.21	00:08:39.03	16	35	7
5	26	00:08:54.23	n	smartie	h			Yes	Yes											00:08:55.15	00:08:57.01	00:08:57.07	17	36	6
5	27	00:09:16.08	n	cabbage	l			No	Yes	Yes		Yes					Yes			00:09:17.08	00:09:18.02		25	19	
5	28	00:09:39.00	n	malteser	h			Yes	Yes	Yes										00:09:39.17	00:09:40.08	00:09:41.14	17	16	31
5	29	00:10:00.23	n	orange	h			No	No																
5	30	00:10:33.00	n	apricot	h			No	Yes	Yes										00:10:33.21	00:10:34.11	00:10:34.15	21	15	4
5	31	00:10:51.07	n	chocolate raisin	h			Yes	Yes	Yes										00:10:52.01	00:10:52.18	00:10:53.03	19	17	10

5	32	00:11:15.02	n	white grape	h			Yes	Yes	Yes										00:11:15.21	00:11:16.11	00:11:16.17	19	15	6
5	33	00:11:35.06	c	malteser	h	cabbage	l	Yes	Yes										Yes	00:11:35.23	00:11:39.23		17	100	
5	34	00:12:04.08	n	smartie	h			Yes	Yes					Yes		Yes				00:12:05.01	00:12:07.00	00:12:07.10	18	49	10
5	35	00:12:34.08	n	apple	l			No	Yes	Yes										00:12:35.03	00:12:35.19	00:12:36.02	20	16	8
5	36	00:12:54.04	n	greengage	h			No	Yes							Yes			Yes	00:12:54.22	00:12:55.16	00:12:55.23	18	19	7
5	37	00:13:21.13	n	white grape	h			No	No					Yes											
5	38	00:13:44.24	n	chocolate raisin	h			No	No																
5	39	00:14:19.01	n	apricot	h			No	No								Yes								
5	40	00:14:49.15	n	chocolate raisin	h			No	No								Yes								
5	41	00:15:22.12	n	malteser	h			Yes	Yes	Yes										00:15:23.05	00:15:23.20	00:15:24.01	18	15	6
5	42	00:15:42.15	n	apricot	h			No	No																
5	43	00:16:07.16	n	smartie	h			No	No								Yes	Yes							
5	44	00:16:41.10	n	greengage	h			No	No					Yes		Yes	Yes	Yes							

APPENDIX B

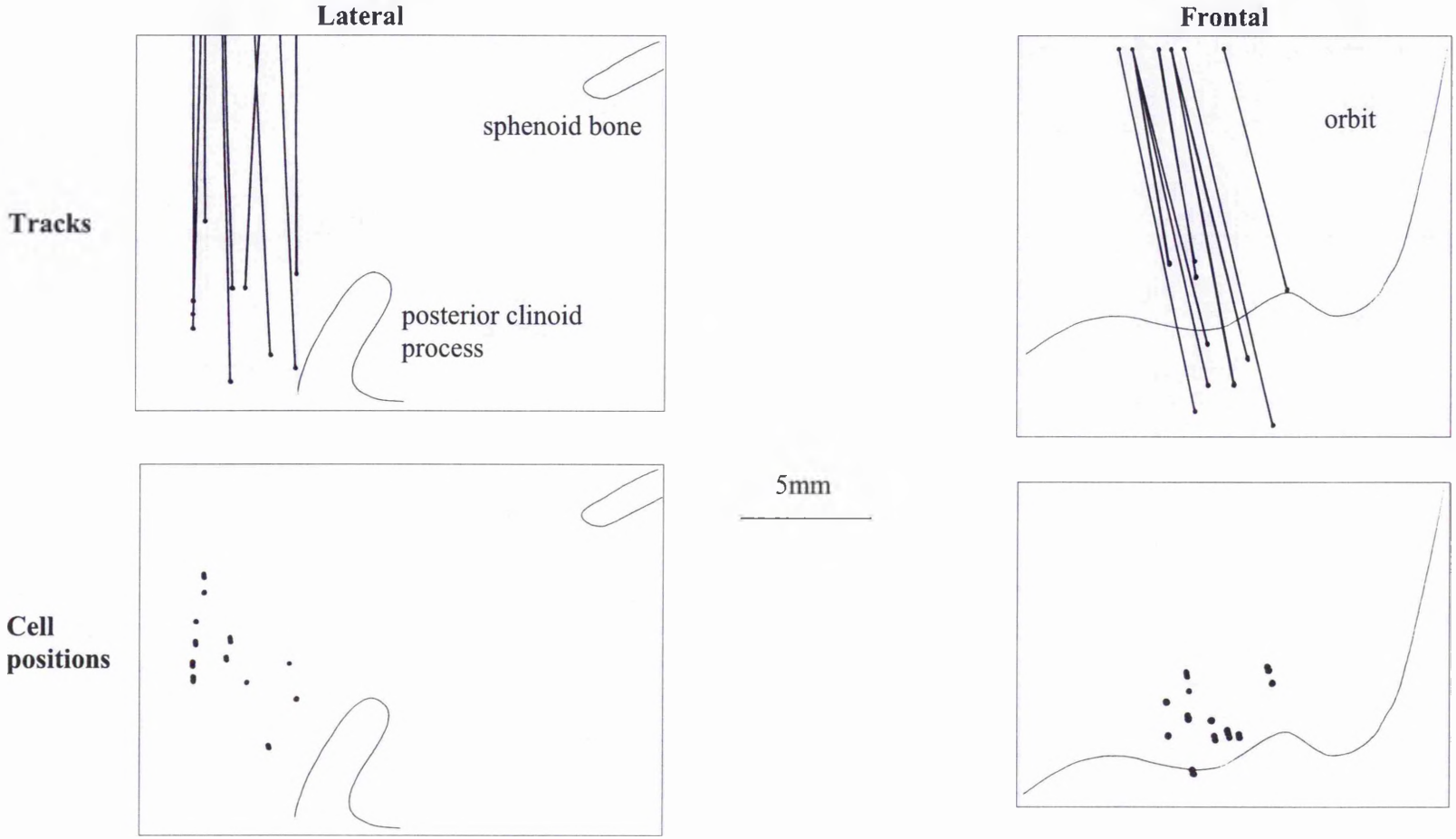
X-RAY RECONSTRUCTION OF ELECTRODE TRACKS

The figures on the following pages show the x-ray reconstructions of the recording tracks for each of the populations of cells described in the thesis, for each monkey subject (Steve: figures B1-B3; Terry: figures B4-B6). The reconstructions are plotted in x-ray co-ordinates and represent approximately a 12% enlargement over life-size. The left column on each page shows the reconstructions from the lateral x-rays, and the column on the right shows the reconstructions from the frontal x-rays. The top row shows the trajectories of the recording tracks, and the bottom row, the positions of individual cells.

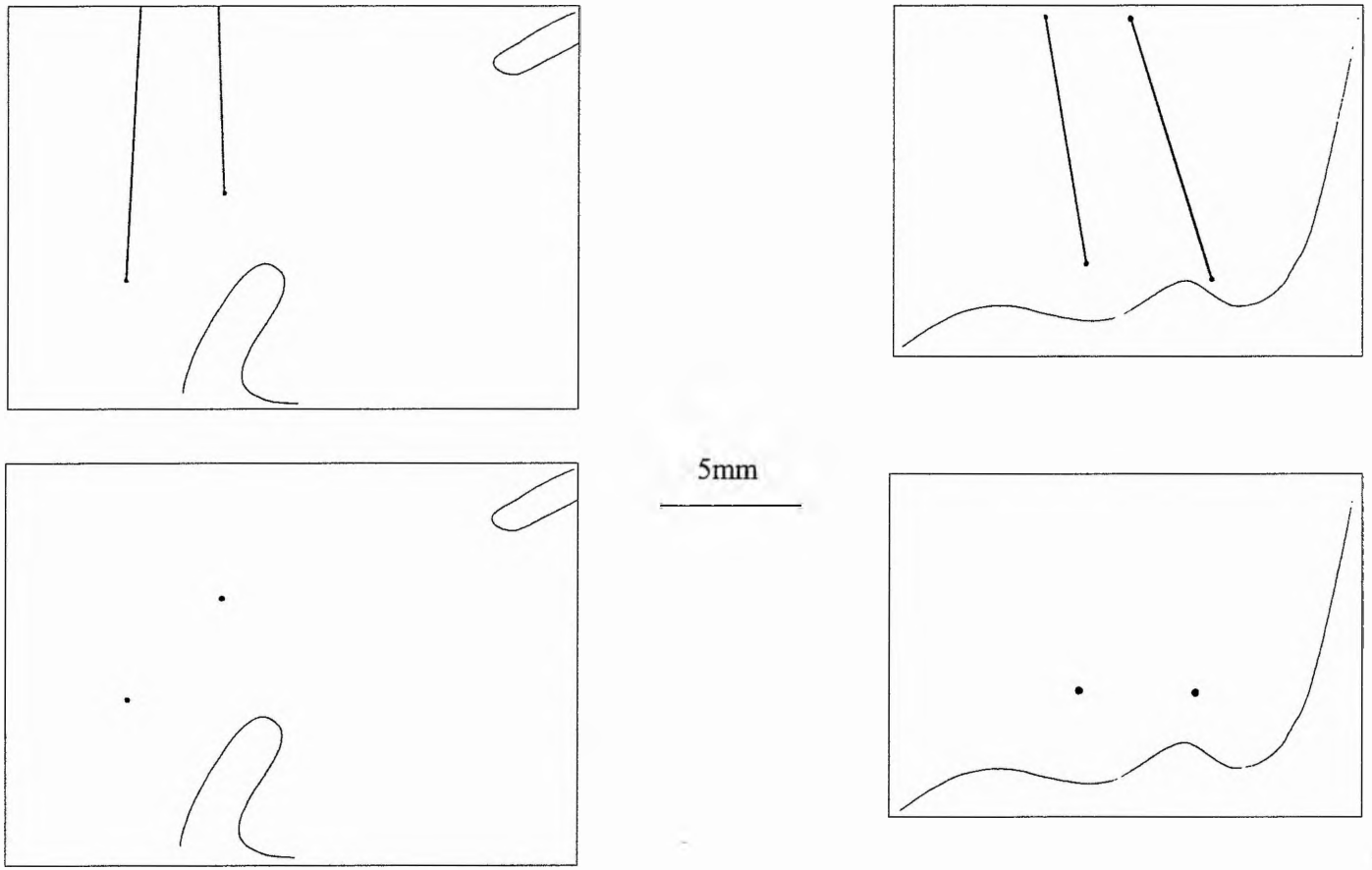
The final figure (B7) shows the reconstruction from the lateral and frontal x-rays of the final recording track in one of the subjects (Steve). The electrode was coated with fluorescent marker (DiI) and a micro-lesion was made at the final recording position. The position of this track can be aligned with both histology and structural MRI (see appendix C).

All three populations of cells were co-extensive in each subject. Comparison of the reconstructions for each subject shows that the cells were recorded at a slightly more lateral position and at a lesser depth in Terry than Steve. The anterior-posterior position was comparable in each subject, the recordings made just posterior to the posterior clinoid process. In comparing the x-rays between subjects, however, it is important to note that slight differences in the location and angle of the head cap and position of fixation in the primate chair may lead to a different head orientation for the x-rays, making across-subject comparisons difficult.

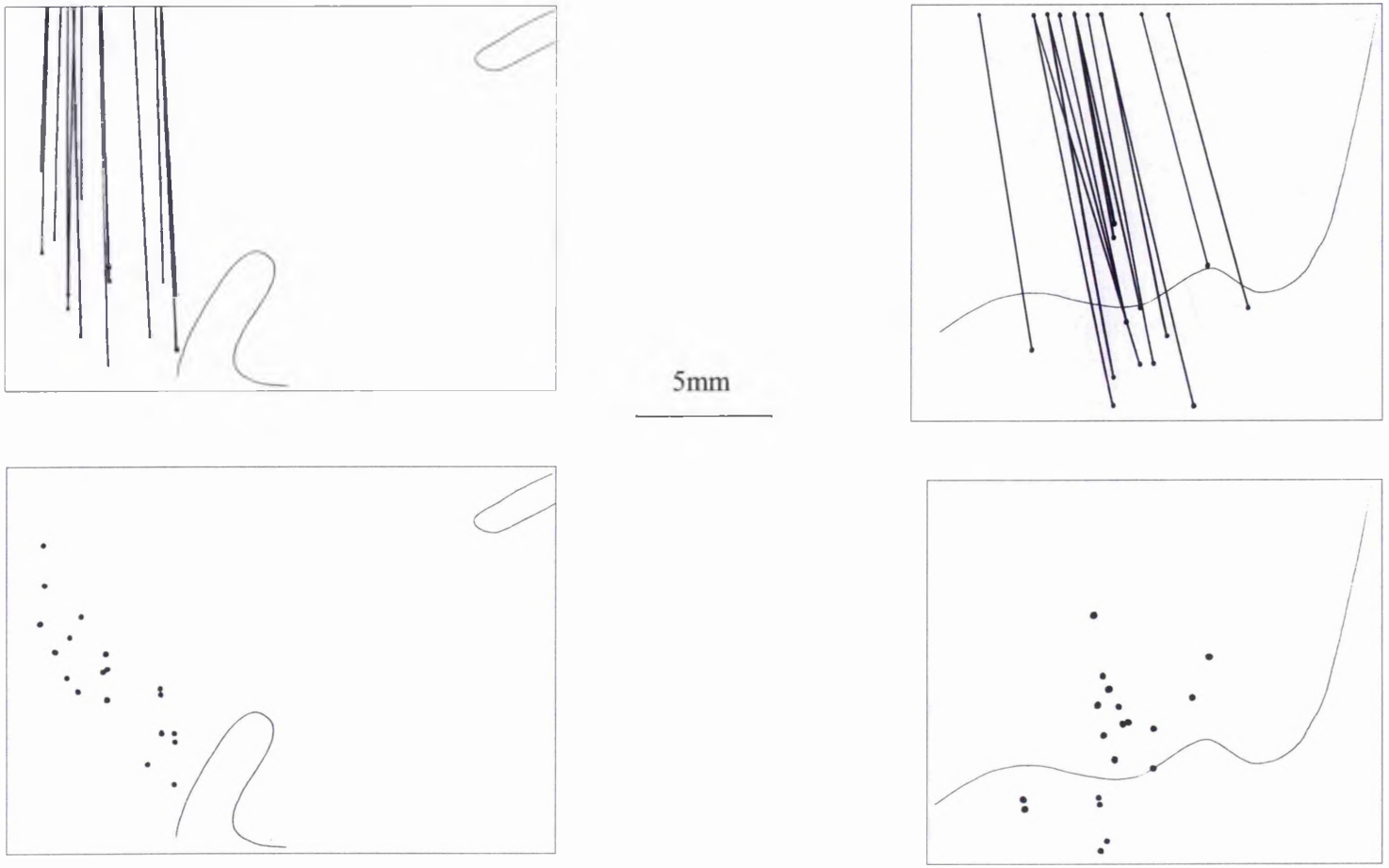
The x-rays are comparable with those of previous subjects of neurophysiological recordings in which localization within STS was confirmed histologically. The amygdala is sited just anterior to the posterior clinoid process (Aggleton and Passingham, 1981), locating the current recordings to an anterior-posterior position just behind the amygdala.



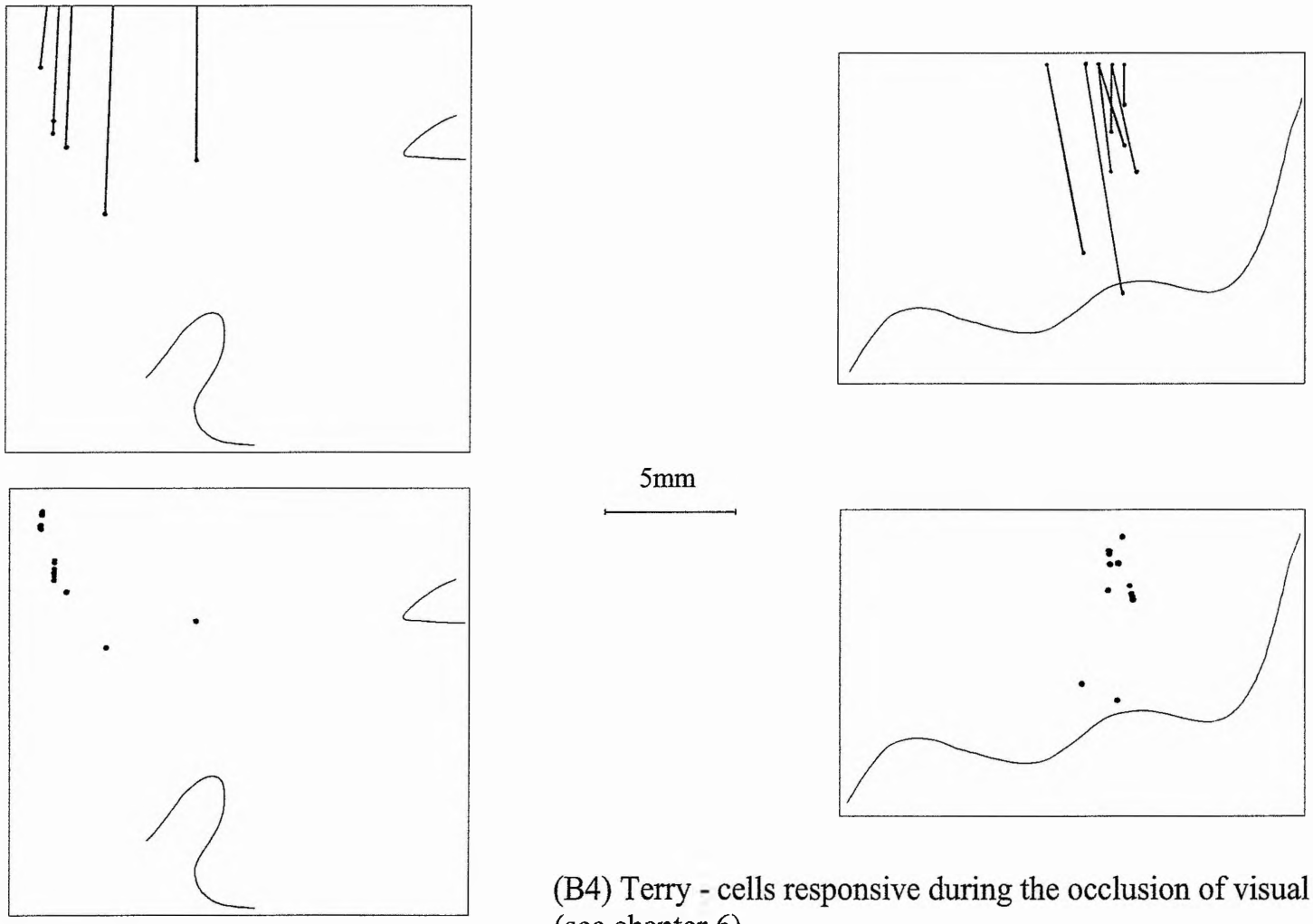
(B1) Steve - cells responsive during the occlusion of visual stimuli (see chapter 6).



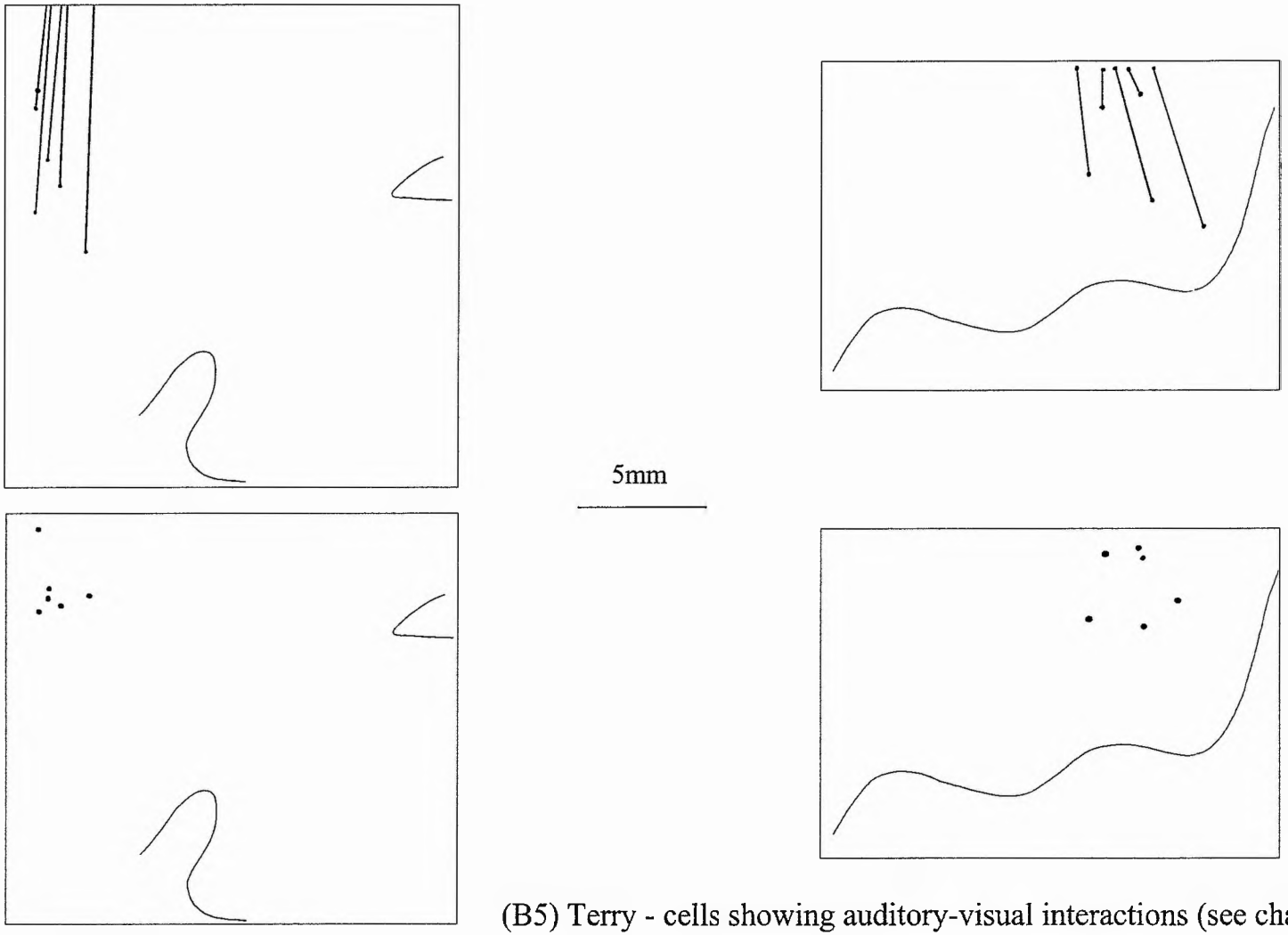
(B2) Steve - cells showing auditory-visual interactions (see chapter 7).



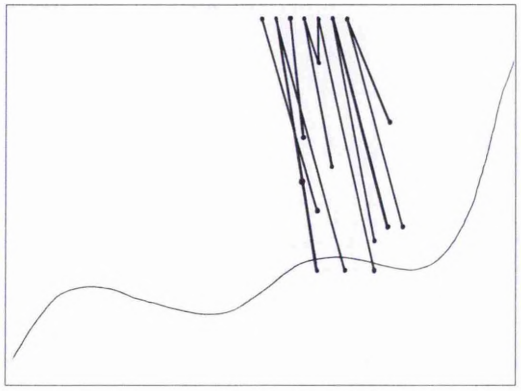
(B3) Steve - cells showing selectivity for the position of stimuli (see chapter 8).



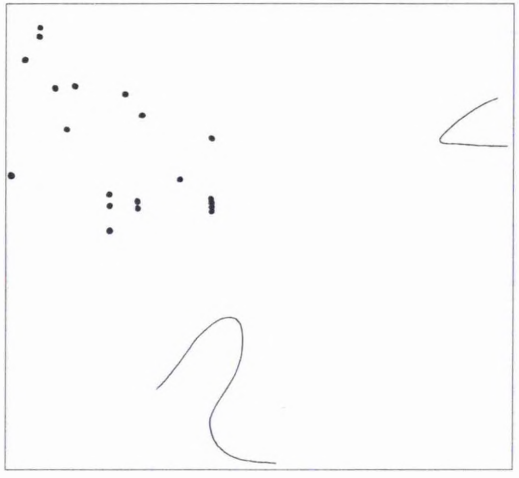
(B4) Terry - cells responsive during the occlusion of visual stimuli (see chapter 6).

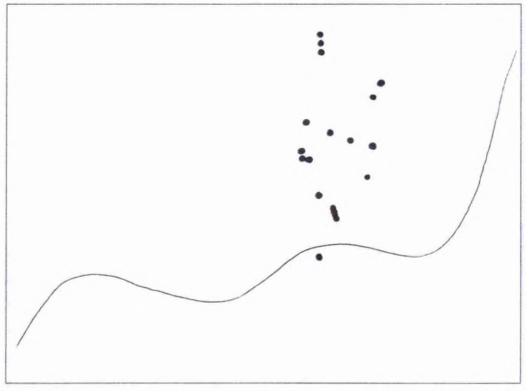


(B5) Terry - cells showing auditory-visual interactions (see chapter 7).

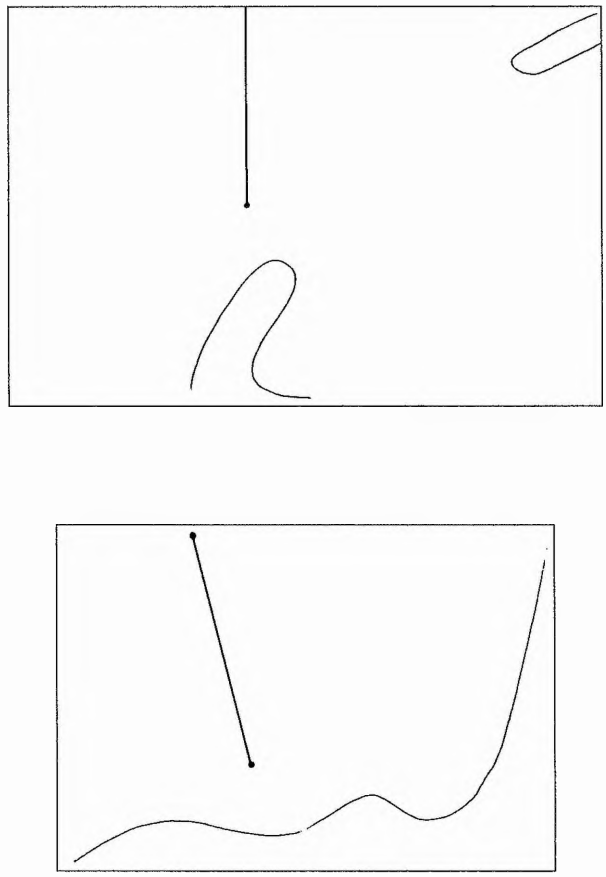


5mm





(B6) Terry - cells showing selectivity for the position of visual stimuli (see chapter 8).

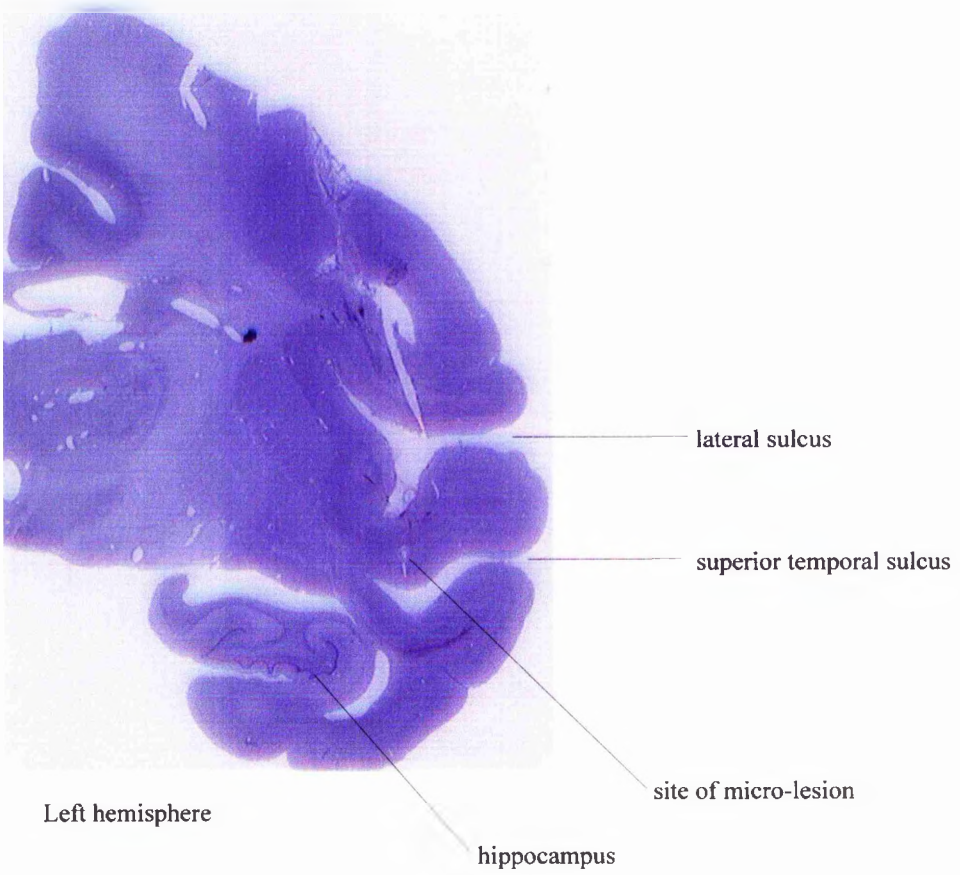


(B7) Position of the final recording track in Steve, labelled with fluorescent dye and marked with a micro-lesion. Relative to the cell populations described, the lateral position and depth of this track are comparable, although it is at a slightly more anterior position.

APPENDIX C

HISTOLOGY

The figure on the following page shows a Nissl stained section from the brain of one of the monkey subjects (Steve). The site of the micro-lesion is clearly visible in the upper bank of the superior temporal sulcus. This site was confirmed with visualization of the DiI fluorescent marker. The uncus of the hippocampus is visible, showing that this section was made just posterior to the amygdala.



Left hemisphere

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